Frasnian gastropod synecology and bio-events in the Dyminy reef complex of the Holy Cross Mountains, Poland

WOJCIECH KRAWCZYŃSKI

Krawczyński, W. 2002. Frasnian gastropod synecology and bio-events in the Dyminy reef complex of the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* 47 (2): 267–288.

Frasnian gastropods from the Kowala Formation (north-western part of the Holy Cross Mountains, Poland) form five reef associations and one lagoonal assemblage are described. The distinct influence of regional shallowing-upward cycles on the composition of gastropod fauna have been observed. Composition changes of this fauna were controled by IIb/c, IIc, and IId cycles. Early Frasnian reef association appeared with predominantly thick-shell gastropods, which occur in the upper Sitkówka Beds. At the beginning of IIb/c cycle, Kadzielnia-type mud mounds with a high diversified gastropod association appeared. The next cycles caused the disappearance of mud mounds (IIc), the sinking of the Dyminy reef (IId), and extinction of the gastropod associations from the upper Sitkówka Beds. Two gastropod associations and one poorly diversified lagoonal assemblage predominated in the reef-cap stage. Frasnian reef gastropods have not been observed in the Famennian and Early Carboniferous series. Thus, they probably became extinct together with the collapse of the Frasnian reef ecosystem near the Frasnian–Famennian boundary. Twenty seven taxa have been recognized, among them three new species and two new genera are described: *Kowalatrochus sanctacrucensis* gen. et sp. nov., *Grabinopsis guerichi* gen. et sp. nov., and *Loxoplocus* (*Donaldiella*) *karczewskii* sp. nov. Two poorly known Gürich's species have been also revised: *Euryzone kielcensis* and *Orecopia kadzielniae*.

Key words: Gastropoda, Devonian, taxonomy, palaeoecology, Frasnian–Famennian extinction, Poland.

Wojciech Krawczyński [wojtekk@us.edu.pl], Wydział Nauk o Ziemi, Uniwersytet Śląski, ul. Będzińska 60, PL-41-200 Sosnowiec, Poland.

Introduction

Devonian gastropods, which mostly occur in reef and lagoonal facies, are very poorly known, especially from palaeoecological and evolutionary viewpoints. There is a lack of data regarding the history of this group during the major extinction time of reef ecosystems at the Frasnian–Famennian boundary (McGhee 1996). Extensive new material collected in Frasnian sequences of the Holy Cross Mountains allowed more detailed investigations of the gastropods.

Frasnian gastropods from the Holy Cross Mountains were first described by Pusch (1837). One of them is *Buccinum vetustum* which is from the Frasnian limestone at Karczówka hill in Kielce. Gürich (1896) presented more detailed descriptions of Frasnian gastropods. He has depicted eleven Frasnian species, including four new ones: *Pleurotomaria kadzielniae*, *Pleurotomaria cardiolae*, *Polytropis kielcensis*, and *Loxonema polonicum*. There are a lot of works with notices on the occurrence of Frasnian gastropods (e.g., Siemiradzki 1909; Sobolev 1909, 1912; Stasińska 1953; Kaźmierczak 1971; Szulczewski 1971; Różkowska 1980; Racki 1988, 1993b; Karczewski 1992). Karczewski (1980, 1989) published two papers about Devonian gastropods from the Holy Cross Mountains where he also took into account Frasnian taxa. In the present paper some of the Karczewski's determinations are corrected. The history of development of gastropod fauna is studied in context of Frasnian global events.

Geological settings

The Holy Cross Mountains are divided into the three main palaeogeographical units: the Łysogóry region, Kielce region, and the Kostomłoty transitional zone between them (Szulczewski 1971, 1995; Racki 1993b, 1997). Frasnian gastropods occur mainly in the rocks of the Kielce region, which has been divided (Racki 1993b) into four subregions: Northern, Central, Southern, and Chęciny-Zbrza. The studied material was collected from the first three subregions: Northern (Kadzielnia, Karczówka, Grabina, Szczukowskie Górki), Central (Sitkówka-Kowala, Sitkówka-Jaźwica, Panek), and Southern (Kowala, Jaźwica) (Fig. 1). That division is connected with a visually symmetric Frasnian reef structure, which is called the "Dyminy reef". A shoal corresponding to the Central Kielce subregion is recognized, and the slopes are

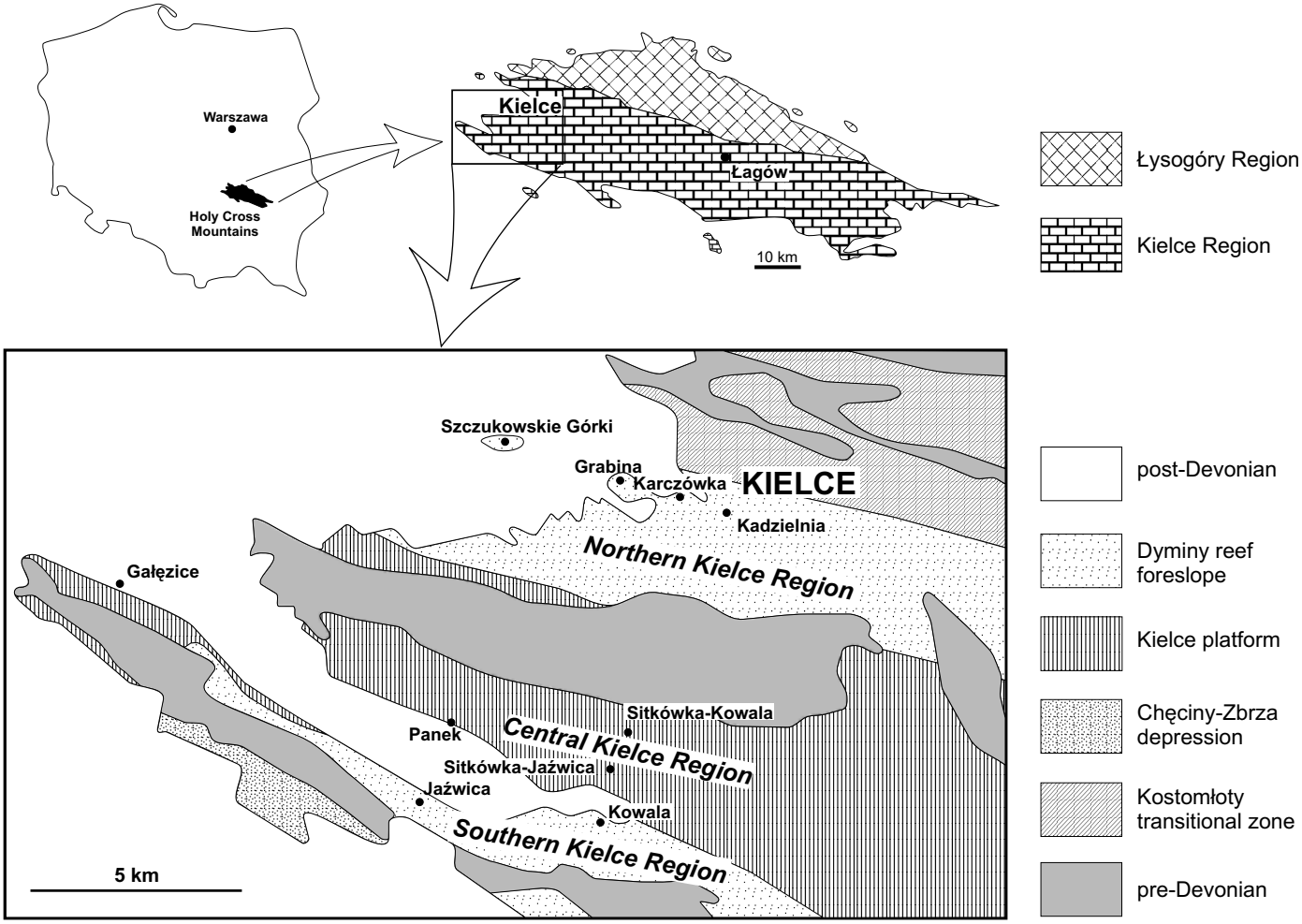

Fig. 1. Location of studied sites in the western part of the Holy Cross Mountains against the background of early Frasnian facies distribution (after Racki 1993b).

consequently recognized in the Northern and Southern Kielce subregions (Fig. 2; see Racki 1993b).

The history of the reef evolution was scrutinized by Racki (1993b) and Szulczewski (1995). The middle Givetian agraded *Stringocephalus* bank was drowned in the late Givetian (cycle IIb; *sensu* Johnson et al. 1985; see also Racki 1997; Fig. 2), and a stromatoporoid-coral biostromal complex appeared (lower Sitkówka Beds; see Kaźmierczak 1971; Szulczewski 1971; Racki 1993b, 1997; Fig. 2). A large transgressive pulse in the early Frasnian (Early *Palmatolepis punctata* Zone) caused the appearance of the symmetrical reef structure (the upper Sitkówka Beds) surrounded by Kadzielnia-type mud mounds and the Detrital Beds. The strongest transgressive pulse (IId *sensu* Johnson et al. 1985), connected with anoxic Kellwasser events (Walliser 1996), contributed to the disappearance of the reef structure (*Pa. rhenana* Zone) and its covering by the reef cap, as well as to its total extinction before the Frasnian–Famennian boundary (see Narkiewicz 1987; Racki 1990; Fig. 2).

The gastropods can be mostly found in biolithites and organodetrital limestones and less often in marly limestones (Fig. 3; for detailed lithostratigraphic terminology, including set definitions, see Racki 1993b). Locations with gastropod faunas are concentrated in the Frasnian Kowala Formation sets, detrital beds and lower Frasnian mud mounds (Fig. 2).

Material

Most of investigated material (about 300 specimens) was collected by the author during field trips in 1995–2000. Fourty specimens were collected by Racki in 1976–1994 and later initially studied by Karczewski (1989). The gastropod collection from the Institute of Palaeobiology of the Polish Akademy of Science, Warsaw (abreviated ZPAL), and gastropods from the original collection of Gürich (1896) deposited at the Geological Museum of the Institute of Geological Sciences of Wrocław University (abreviated MGUWr), have also been studied. The author's collection as well as Racki's specimens are housed at the Faculty of Earth Sciences of Silesian University, Sosnowiec (abreviated GIUS).

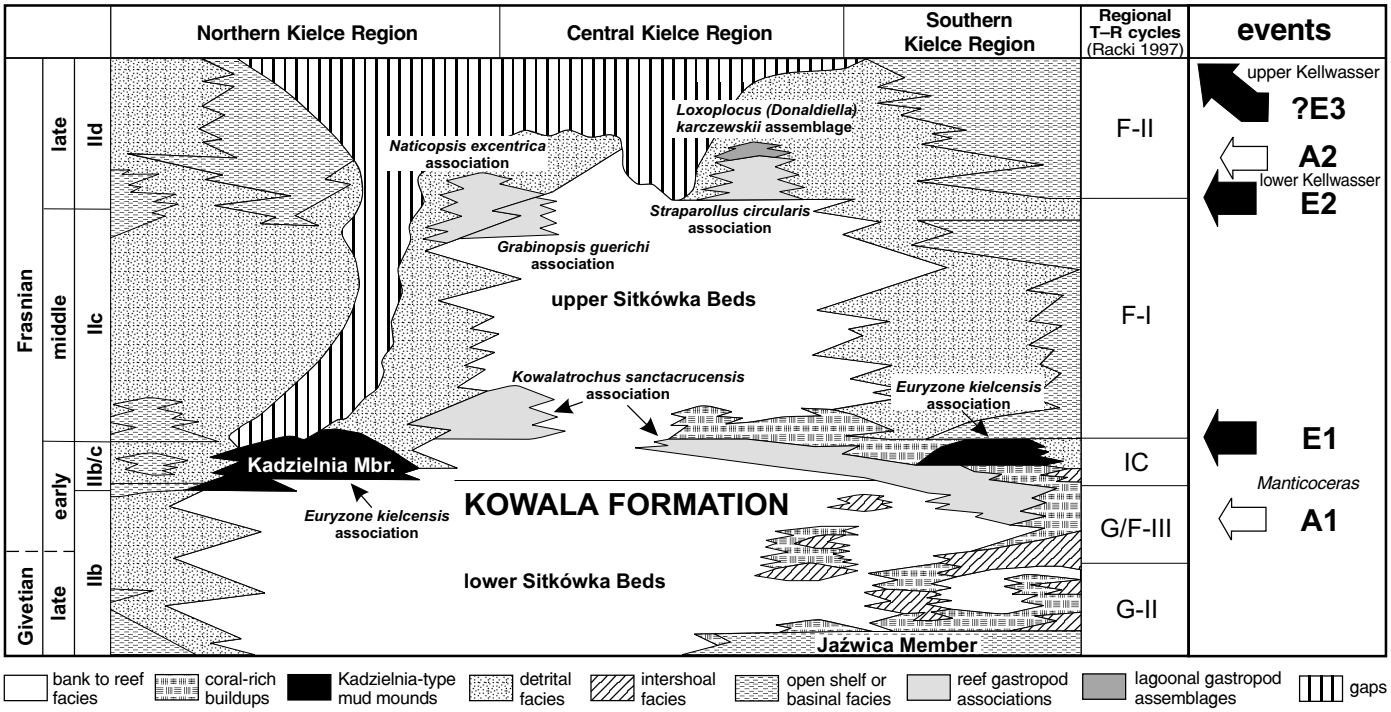

Fig. 2. Localization of described sequences including gastropod fauna against the background of a late Givetian to late Frasnian idealized stratigraphic-facies cross-section of the Holy Cross Mountains (after Racki 1993b) with gastropod appearance (A) and extinction (E) events (Krawczyński 1999).

Taxonomic review of gastropods

Abbreviations used: H/W, height to width of the shell ratio; H_w/W_w, height to width of a whorl ratio; H_a/W_a, height to width of the aperture ratio.

Euomphaloideans

***Straparollus* (*Straparollus*) *serpens* (Phillips, 1841)** (Fig. 4E).—Eleven specimens of the discoidal shell of this species and some fragments of its spire have been found in the middle Frasnian upper Sitkówka Beds of Grabina (set A) and in the late Frasnian Detrital Beds of Panek (set B_2) and Grabina (set C).

***Straparollus* (*Straparollus*) *circularis* (Phillips, 1841)** (Fig. 4A, B).—Relatively large shells (diameter to 5 cm) with a distinct peripheral ridge on the last whorl and with septation in the older part of spire occur in the Kadzielnia Member (Kadzielnia, set A) and in the Detrital Beds (Panek, set B_2; Grabina, set C).

Pleurotomarioideans

***Liospira* sp.** (Fig. 5G, H).—A fragment of a discoidal shell with a selenizone at the periphery of the whorl has been found in the middle Frasnian upper Sitkówka Beds (Grabina, set B).

***Villmaria ventricosa* Heidelberger, 2001** (Fig. 4G).—Species of recently erected genus *Villmaria* Heidelberger, 2001. Five well preserved turbiniform shells and six shell fragments are present, which are characterized by a gradate spire with a gently projecting selenizone just above the whorl periphery. The shells have spiral ornamentation on the inclined ramp and a rounded convex base (see also Heidelberger 2001). *V. ventricosa* was recognized in the upper Sitkówka Beds (Grabina, set B; Kowala, set A) as well as in the Kadzielnia Member (Kadzielnia, set A) and the Detrital Beds of Grabina (set C).

***Loxoplocus* (*Donaldiella*) *karczewskii* sp. nov.** (Fig. 6A–E).—See description on p. 273.

***Lahnospira taeniata* (Sandberger, 1842)** (Fig. 4M).— Species of recently erected genus *Lahnospira* Heidelberger, 2001. A few specimens of *L. taeniata*, the shell having a turbiniform shape with a wide protruding selenizone (see also Heidelberger 2001), were found in the middle Frasnian of the upper Sitkówka Beds (Grabina, set B).

***Euryzone kielcensis* (Gürich, 1896) comb. nov.** (Fig. 7I–L).—See description on p. 274.

***Coelozone* sp.** (Fig. 8N).—Two fragments of a shell with a wide selenizone just above the suture have been established in the upper Sitkówka Beds at "Kowala" quarry (lower Frasnian, set A_2).

Cirroideans

***Porcellia bifida* (Sandberger and Sandberger, 1850–1856)** (Figs. 4L, 7A–C).—Four relatively well preserved pseudo-

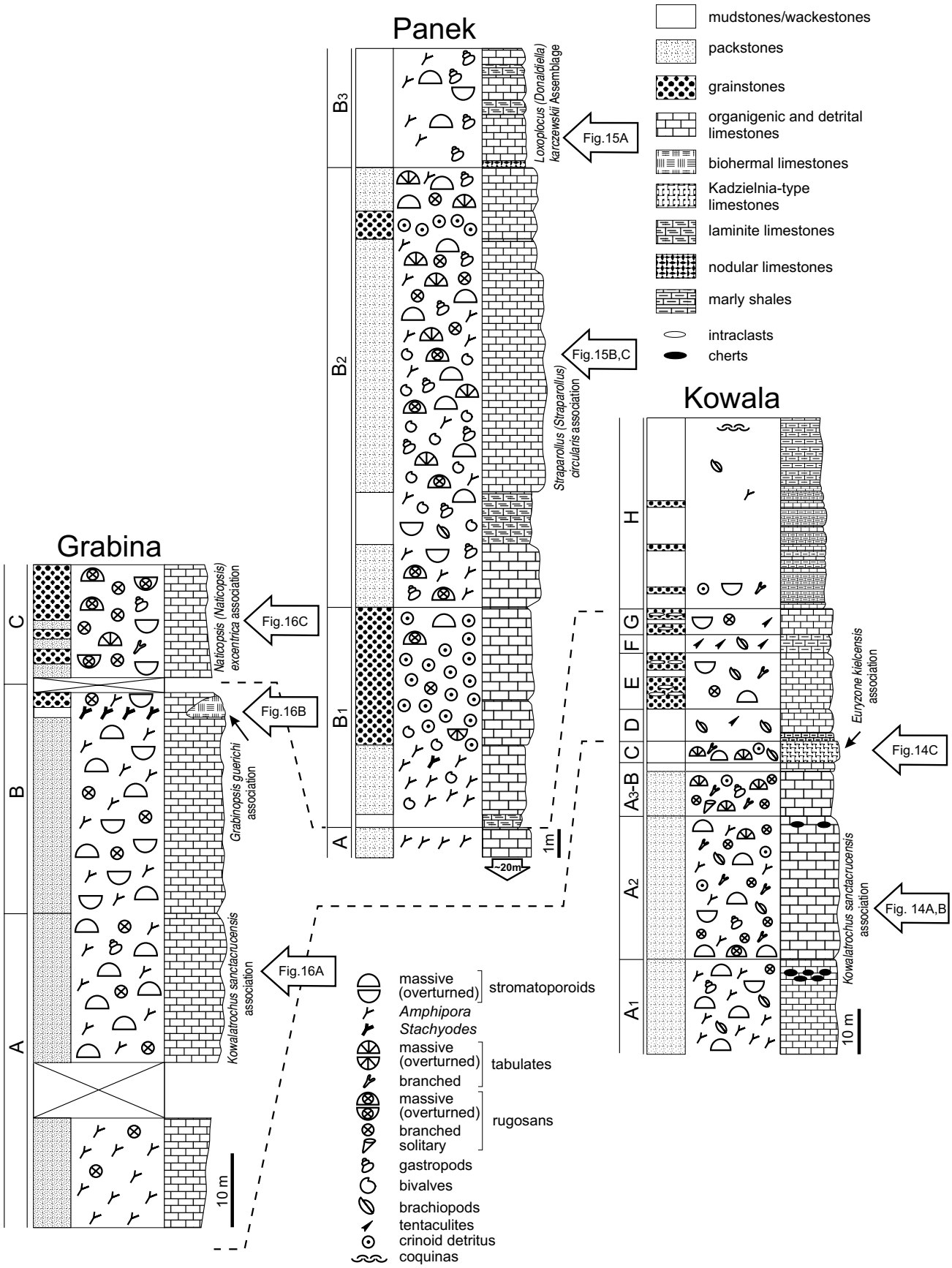

Fig. 3. Correlation of reference sections representing the Northern (Grabina), the Central (Panek), and the Southern (Kowala) Kielce Region with faunal composition, and lithology (after Kaźmierczak 1971; Szulczewski 1971; Coen-Aubert and Wrzołek 1991; Racki 1993b; Krawczyński 1998).

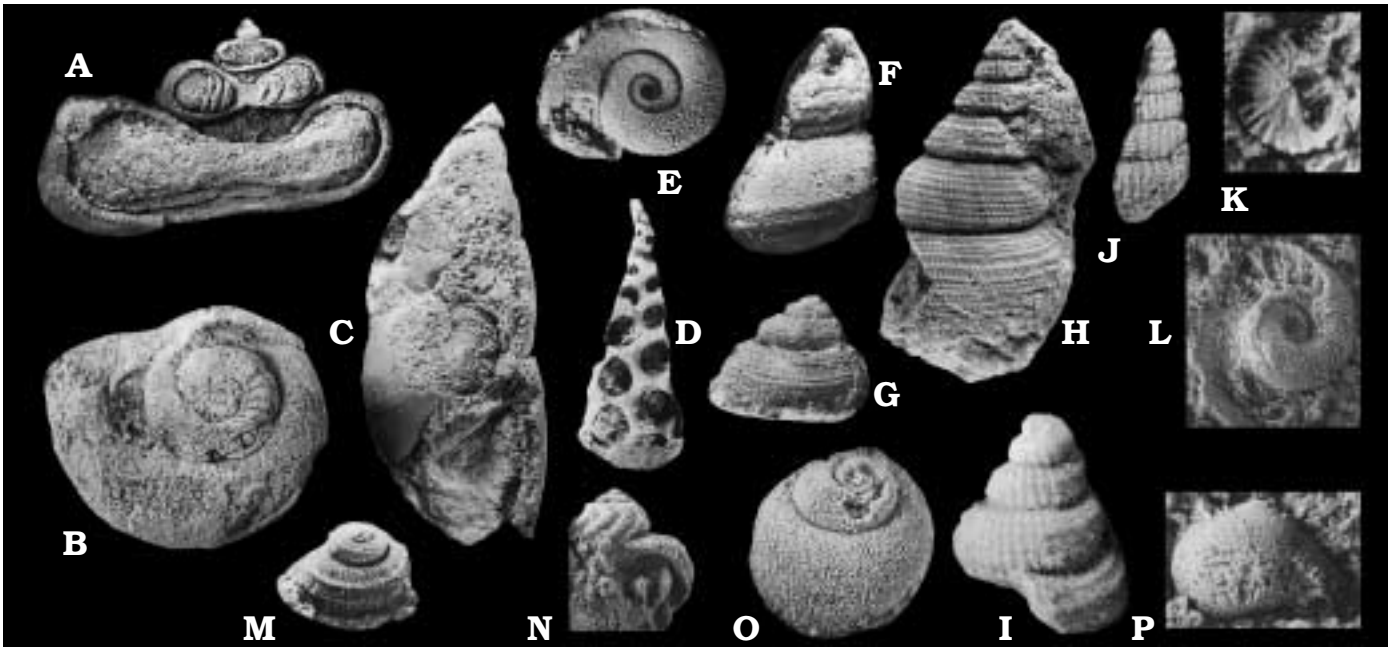

Fig. 4. Late Frasnian gastropod associations: *Straparollus* (*Straparollus*) *circularis* of the *Actinostroma* Assemblage and *Naticopsis* (*Naticopsis*) *excentrica* of the *Frechastrea pentagona* Assemblage (the Detrital Beds). **A**, **B**. *Straparollus* (*Straparollus*) *circularis* (Phillips, 1841), both natural size. **A**. Axial section with visible septation of spire, GIUS 4-1463/Pan-80. **B**. Apical view of poorly preserved shell with septation of spire, GIUS 4-1440/Pan-57. **C**. *Westerna subcostata* (Schlotheim, 1820) comb. nov., apertural view of poorly preserved shell, GIUS 4-854/Pan-1, natural size. **D**. *Murchisonia* sp., axial section, GIUS 4-1444/Pan-61, × 2. **E**. *Straparollus* (*Straparollus*) *serpens* (Phillips, 1841), lateral view of shell, GIUS 4-877/Gr-9/2, × 3. **F**. *Murchisonia* (*Murchisonia*) *nerinea* (Sandberger and Sandberger, 1850–1856), fragment of spire, GIUS 4-999/Gr-131/4, × 4. **G**. *Villmaria ventricosa* Heidelberger, 2001, lateral view of shell (GIUS 4-1010/Gr-142/1), × 4.5. **H**, **I**. *Roemeriella octocincta* (Roemer, 1843), lateral views of spires, Szczukowskie Górki quarry. **H**. Coeloconoidal shell with change of ornamentation, GIUS 4-1203/SzG-8, × 2. **I**. Juvenile spire, GIUS 4-1204/SzG-10, × 4. **J**. *Palaeozygopleura* (*Rhenozyga*) sp. B, lateral view of shell, GIUS 4-906/Gr-38, × 4. **K**. *Palaeozygopleura* (*Rhenozyga*) sp. A, base of shell with ornamentation, GIUS 4-1005/Gr-137/1, × 7. **L**. *Porcellia bifida* (Sandberger and Sandberger, 1850–1856), lateral view of spire, GIUS 4-877/Gr-9/10, × 3. **M**. *Lahnospira taeniata* (Goldfuss, 1844), lateral view of juvenile shell, GIUS 4-1004/Gr-136/5, × 8. **N**. *Naticopsis* (*Naticopsis*) *excentrica* (Roemer, 1843), apertural view of shell with well preserved ornamentation, GIUS 4-902/Gr-34, × 3. **O**. *Naticopsis* (*Naticopsis*) *inflata* (Roemer, 1843), lateral view of spire, GIUS 4-876/Gr-8/1, × 3.5. **P**. *Naticopsis* (*Naticopsis*) *protogaea* (Goldfuss, 1844), apical view of poorly preserved shell, GIUS 4-900/Gr-32, × 3. **A**–**D**. Panek, set B_2. **E**–**G**, **J**–**P**. Grabina, set C.

isostrophic shells were identified from the middle to late Frasnian in the Kadzielnia Member (Kadzielnia, set A; Jaźwica, set J) and in the Detrital Beds of Grabina (set C).

Trochoideans

***Kowalatrochus sanctacrucensis* gen. et sp. nov.** (Fig. 8A–K).—See description on p. 276.

***Roemeriella octocincta* (Roemer, 1843)** (Figs. 4H–I, 7F).—Species of recently erected genus *Roemeriella* Blodgett and Frýda, 1999. Eighteen rather well preserved specimens and 5 fragments of turbiniform shells were collected from the early to middle Frasnian in the Kadzielnia Member (Jaźwica, set J) as well as in the Detrital Beds (Grabina, set C; Szczukowskie Górki).

Teleoconchs have prosoclinal costa on the first 2–3 whorls without spiral ornamentation and four distinct spiral cords with small tubercles appearing on the next 4–6 whorls. The next whorls of the coeloconoidal shell have equal development of both spiral and prosoclinal elements forming a cancellate ornamentation (see also Blodgett and Frýda 1999).

***Roemeriella cyclostomoides* (Roemer, 1854)** (Fig. 5L).—One well preserved specimen and 2 shell fragments were found in the middle Frasnian at Grabina, set B.

Murchisonioideans

***Murchisonia nerinea* (Sandberger and Sandberger, 1850–1856)** (Figs. 4F, 5K).—Two fragments of the spire of *M. nerinea* were found in the upper Sitkówka Beds and the Detrital Beds of Grabina (middle and late Frasnian; set B and C).

***Murchisonia* sp.** (Fig. 4D).—A few specimens with a turriculate spire and a selenizone at the periphery of the whorl have been found in the Kadzielnia Member (Kadzielnia, set A; middle Frasnian) as well as in the Detrital Beds of Panek (set B_2; late Frasnian).

Neritoideans

***Grabinopsis guerichi* gen. et sp. nov.** (Fig. 5A–F).—See description on p. 278.

***Naticopsis* (*Naticopsis*) *inflata* (Roemer, 1843)** (Figs. 4O,

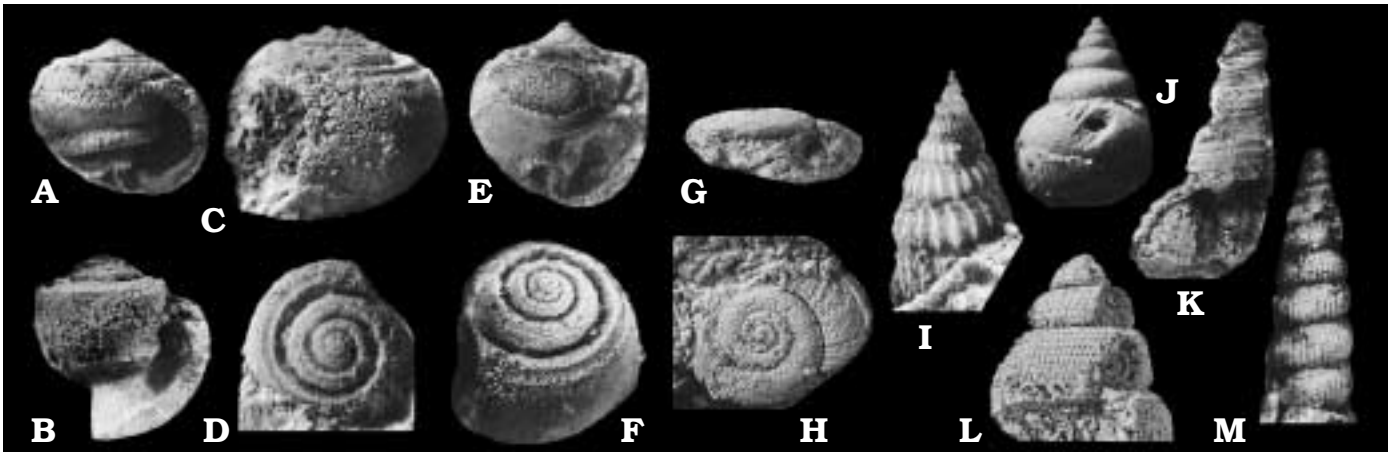

Fig. 5. *Grabinopsis guerichi* association of the *Stachyodes* Assemblage from the upper Sitkówka Beds, Grabina, set B, middle Frasnian. **A**–**F**. *Grabinopsis guerichi* gen. et sp. nov. **A**, **B**. Apertural views of shells with well visible columellar fold. **A**. Holotype, GIUS 4-981/Gr-113, × 8. **B**. GIUS 4-974/Gr-106/1, × 6. **C**. Apertural view of shell with narrow umbilicus, GIUS 4-984/Gr-112/2, × 7. **D**. Lateral view of shell. **E**, **F**. Lateral and apical views of shell, GIUS 4-978/Gr-110/1, × 8. **G**, **H**. *Liospira* sp., apertural and apical views of shell, GIUS 4-953/Gr-85, × 3. **I**. *Palaeozygopleura* (*Rhenozyga*) sp. A, lateral view of spire, GIUS 4-979/Gr-111/4, × 10. **J**. Gen. et sp. ex fam. Subulitidae indet., lateral view of shell, GIUS 4-969/Gr-101/2, × 6. **K**. *Murchisonia* (*Murchisonia*) *nerinea* (Sandberger and Sandberger, 1850–1856), latral view of spire fragment, GIUS 4-969/Gr-101/8, × 5. **L**. *Roemeriella cyclostomoides* (Roemer, 1854), lateral view of spire, GIUS 4-982/Gr-114, × 3. **M**. *Palaeozygopleura* (*Rhenozyga*) cf. *retrostriata* (Kirchner, 1915), lateral view of spire, GIUS 4-974/Gr-106/4, × 6.

7D, E, 8O).—The most common specimens in Frasnian deposits exhibit naticiform shells with a large morphological variation within the species. *N. inflata* has been recognized from early to late Frasnian in the upper Sitkówka Beds (Kowala, set A_2; Grabina, set B; Szczukowskie Górki), in the Kadzielnia Member (Kadzielnia, set A; Jaźwica, set J), and in the Detrital Beds (Grabina, set C; Sitkówka-Jaźwica, set B).

***Naticopsis* (*Naticopsis*) *protogaea* (Goldfuss, 1844)** (Figs. 4P, 8P).—Two fragments of shell with poorly preserved external surface have been found in the upper Sitkówka Beds (Kowala, set A_2) and in the Detrital Beds (Grabina, set C).

***Naticopsis* (*Naticopsis*) *excentrica* (Roemer, 1843)** (Fig. 4N).—Twenty shells of N. excentrica with typical ornamentation, consisting of zigzag costa on the older whorls and moderately collabral cords on later whorls, have been identified from the late Frasnian of Grabina (set C).

Omphalotrochoideans

***Orecopia kadzielniae* (Gürich, 1896) comb. nov.** (Fig. 9A–I). —See description on p. 279.

Loxonematoideans

***Loxonema* sp.**—Two poorly preserved turriculate shells were found in the upper Sitkówka Beds and the Detrital Beds of Grabina (middle and late Frasnian; set B and C).

***Palaeozygopleura* (*Rhenozyga*) cf. *retrostriata* (Kirchner, 1915)** (Figs. 5M, 7H).—Species of recently erected subgenus *Palaeozygopleura* (*Rhenozyga*) Frýda, 2000. Near 20 fragments of small turriculate shells with minute collabral cords on the whorls (see also Frýda 2000) were recognized in the upper Sitkówka Beds (Kowala, set A_2; Grabina, set B; Szczukowskie Górki) and also in the Kadzielnia Member (Jaźwica, set J).

***Palaeozygopleura* (*Rhenozyga*) sp. A** (Figs. 4K, 5I).—Four specimens without protoconchs and some fragments of spire with collabral cords were collected from the Kadzielnia Member (Jaźwica, set J) and also from the upper Sitkówka Beds and the Detrital Beds of Grabina (set B and C).

***Palaeozygopleura* (*Rhenozyga*) sp. B** (Fig. 4J).—This species consists of eight shell fragments lacking protoconchs with a more slightly rounded whorl profile and more densely spaced collabral ribs than *Palaeozygopleura* (*Rhenozyga*) sp. A. This taxon was found in the middle to upper Frasnian in the the upper Sitkówka Beds and the Detrital Beds of Grabina (set B and C).

Subulitoideans

***Macrochilina ventricosa* (Goldfuss, 1844)**.—Two complete subulate shells without ornamentation and five fragments of spire were identified from the middle to late Frasnian in the upper Sitkówka Beds of Szczukowskie Górki and the Detrital Beds of Grabina (set C).

***Westerna subcostata* (Schlotheim, 1820) comb. nov.** (Figs. 4C, 8L–M; see also Figs. 14A, 15B, C).—The largest gastropod of the Polish Devonian, whose turriculate shells can reach even 20 cm in height, was collected from the lower to upper Frasnian in the upper Sitkówka Beds (Kowala, set A_2; Sitkówka-Kowala, set B), the Kadzielnia Member (Kadzielnia, set A), and the Detrital Beds of Panek (set B_2). The material includes 68 specimens.

Earlier this species was assigned to *Macrocheilus* Phillips, 1841 or *Macrochilina* Bayle, 1880. However, the high turriculate shell with a rounded base, as well as the initial prosoclinal shape of the labrum (and growth lines) that subsequently becomes orthoclinal, and the weakly developed siphonal notch due to the absence of the columellar fold are typical features for the Frasnian genus *Westerna*.

***Spanionema scalaroides* (Whidborne, 1889)** (Fig. 7G).—One well preserved shell and a fragment of a spire with the typical varices have been found in the Kadzielnia limestone at Kadzielnia (set A) and in the upper Sitkówka Beds of Szczukowskie Górki.

gen. et sp. ex fam. Subulitidae indet. (Fig. 5J).—Poorly preserved unidentified subulitids were found from early to late Frasnian in the upper Sitkówka Beds (Kowala, set A_2; Grabina, set B) and the Detrital Beds (Kowala, set E; Grabina, set C).

Description of new and poorly known species

Superfamily Pleurotomarioidea Swainson, 1840
Family Lophospiridae Wenz, 1938
Subfamily Lophospirinae Wenz, 1938
Genus *Loxoplocus* Fischer, 1885

Remarks.—Turriculate shells with V-shaped notch forming a narrow convex selenizone at the middle of whorl belong to genus *Loxoplocus*. Three subgenera are distinguished according to their spire height and the disjunction of their whorls. The protoconch of *Loxoplocus* is not known. Ontogenic development of teleoconch is equal except for the subgenus *Loxoplocus* (*Loxoplocus*) Fischer, 1885, which is marked by the disjunct whorls in the gerontic stage.

Subgenus *Loxoplocus* (*Donaldiella*) Cossmann, 1903

Type species: *Loxoplocus* (*Donaldiella*) *filosa* (Donald, 1902); the Late Ordovician, Scotland.

Remarks.—*Loxoplocus* (*Donaldiella*) is distinguished by its distinctly turriculate spire, whilst the similar *L.* (*Lophospira*) Whitfield, 1886 has a relatively lower turbiniform shell. The shell of *L.* (*Loxoplocus*) differs from both *L.* (*Lophospira*) and *L.* (*Donaldiella*) by its disjunct whorls. Species of *L.* (*Donaldiella*) are singled out on the basis of its relative spire height, apertural shape, and depth of the notch.

Loxoplocus (*Donaldiella*) *karczewskii* sp. nov.

Fig. 6A–E.

Stegocoelia (*Hypergonia*) sp.; Karczewski, 1980: 51, pl. 1: 5–6.

Holotype: GIUS 4-1293/Pan-21 (Fig. 6A).

Type horizon and locality: Active quarry "Panek", set B_3, the Detrital Beds; late Frasnian.

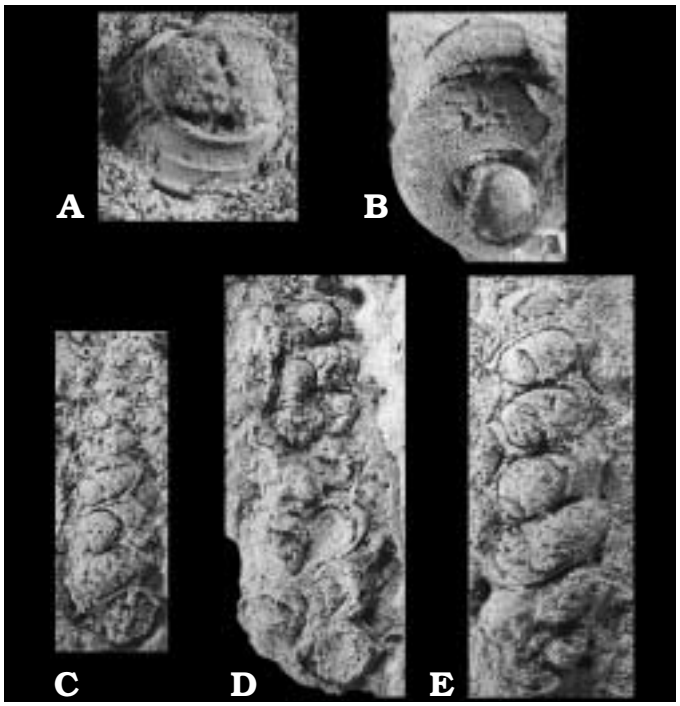

Fig. 6. *Loxoplocus* (*Donaldiella*) *karczewskii* sp. nov. from late Frasnian Detrital Beds, Panek, set B_3. **A**, **B**. Fragments of spire with well preserved ornamentation. **C**–**E**. Spires with visible septation and unpreserved ornamentation. **A**. Holotype, GIUS 4-1293/Pan-21. **B**. GIUS 4-1287/Pan-15. **C**. GIUS 4-1288/Pan-16. **D**. GIUS 4-1292/Pan-20. **E**. GIUS 4-1301/Pan-29. **A**–**C**, **E**. × 2. **D**. × 1.7.

Derivation of the name: In memory of Dr. Leon Karczewski—investigator of fossil snails.

Material.—Fourteen spire fragments without a preserved aperture or older part of the shell (GIUS 4-1285–1288/P13–16, 4-1292–1301/Pan-20–29).

Diagnosis.—High turriculate shell with rounded aperture; narrow distinctly prominent selenizone at the periphery of the whorl. Septation present in the older part of the spire. *Loxoplocus* (*Donaldiella*) *karczewskii* sp. nov. differs from the type species *L.* (*Donaldiella*) *filosa* (Donald, 1902) by its more slender spire and more prominent selenizone. The Late Silurian *L.* (*Donaldiella*) *morinensis* Horný, 1952 has an oval aperture and a differing whorl profile.

Description.—Shell turriculate (about 10 cm in height), number of whorls unknown; shape of whorl distinctly angular; deep notch in center of outer lip, forming a narrow convex selenizone at the periphery of the whorl; growth lines prosoclinal above selenizone and opisthoclinal below it, base with orthoclinal growth lines; ornamentation consists of a strong spiral cord midway between the suture and periphery on the sutural ramp, anomphalous base with two spiral cords: the first one of which is just above suture and the weak second cord is situated between the periphery and lower suture; aperture rounded; protoconch unknown; septation common in the older part of the spire (see Fig. 15A); pleural angle con-

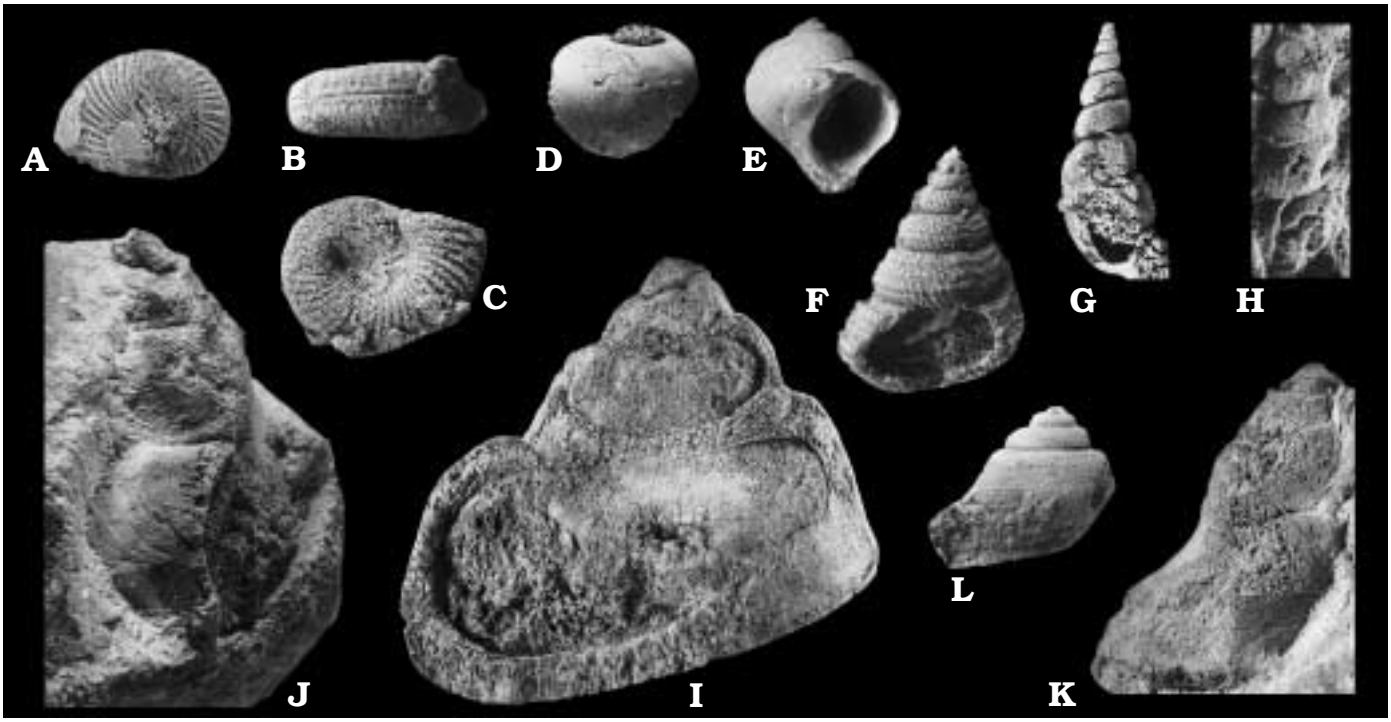

Fig. 7. *Euryzone kielcensis* association of the Kadzielnia-type Assemblage from the Kadzielnia Member (middle Frasnian). **A**–**C**. *Porcellia bifida* (Sandberger and Sandberger, 1850–1856), Jaźwica, set J, × 4. **A**. Lateral view of shell, GIUS 4-1139/Jaź-34. **B**, **C**. Apertural and lateral view of shell, GIUS 4-1140/Jaź-35. **D**, **E**. *Naticopsis* (*Naticopsis*) *inflata* (Roemer, 1843), Kadzielnia, set A. **D**. Lateral view of shell with well preserved growth lines, ZPAL Ga-VI/30, × 2. **E**. Apertural view of shell with well preserved inductura, ZPAL Ga-VI/41, natural size. **F**. *Roemeriella octocincta* (Roemer, 1843), lateral view of shell, Jaźwica, set J, GIUS 4-1129/Jaź-24, × 3. **G**. *Spanionema scalaroides* (Whidborne, 1889), lateral view of shell with well preserved ornamentation, Kadzielnia, set A, GIUS 4-1193/Kad-1, × 2. **H**. *Palaeozygopleura* (*Rhenozyga*) cf. *retrostriata* (Kirchner, 1915), lateral view of spire with poorly preserved ornamentation, Jaźwica, set J, GIUS 4-1159/Jaź-54/1, × 4.5. **I–L**. *Euryzone kielcensis* (Gürich, 1896) comb. nov. **I**–**K**. Lateral views of shell with fragmentary preserved ornamentation, Kadzielnia, set A, GIUS 4-1478/Kad-3, neotype, natural size. **L**. Lateral view of juvenile shell, Jaźwica, set J, GIUS 4-1134/Jaź-29, × 5.

stant (about 12°), variability of the translation index (H_w/W_w) low (Fig. 10).

Remarks.—The first specimens of this new species were described by Karczewski (1980) as *Stegocoelia* (*Hypergonia*) sp. However, the narrow convex selenizone at the periphery proves assignment his specimens to family Lophospiridae. The genus *Loxoplocus* has been recognized from the Ordovician and Silurian as well as from the Early Devonian (Horný 1952; Linsley 1968). The location of investigated specimens has allowed extension of the stratigraphic distribution of the genus *Loxoplocus* from the Ordovician to the late Frasnian.

Distribution.—Holy Cross Mountains: Panek, set B_3 (the Detrital Beds; late Frasnian).

Family Gosseletinidae Wenz, 1938
Subfamily Coelozonidae Knight, 1956
Genus *Euryzone* Koken, 1896

Type species: *Euryzone delphinuloides* (Schlotheim, 1820); Middle Devonian, Germany.

Remarks.—The genus *Euryzone* contains species with trochiform shells and a wide, gently concave selenizone not bordered by spiral cords at the centre of the whorl ramp. The ontogenetic development of the spire is equal or with an increasing pleural angle.

Euryzone kielcensis (Gürich, 1896) comb. nov.

Fig. 7I–L.

Polytropis kielcensis sp. nov.; Gürich 1896: 310.

Neotype: GIUS 4-1478/Kad-3 (Fig. 7I–K).

Type horizon and locality: Kadzielnia in Kielce, set A—the biohermal Kadzielnia Member; middle Frasnian.

Material.—Two almost complete shells and two spire fragments (ZPAL Ga-VI/28, 33; GIUS 4-1134/Jaź-29, 4-1478/Kad-3).

Revised diagnosis.—Large-sized trochiform shell, narrowly phaneromphalous with a flattened base. Whorl profile with two distinctly rounded angulations: the first just below the suture and the second at the periphery. A steep inclined ramp with wide selenizone at middle of whorl is present between the angulations. The species differs from *E. delphinuloides* by its distinctly higher spire.

Description.—The trochiform shell is large (measurements of neotype: height 55 mm, width 56.5 mm) and slightly

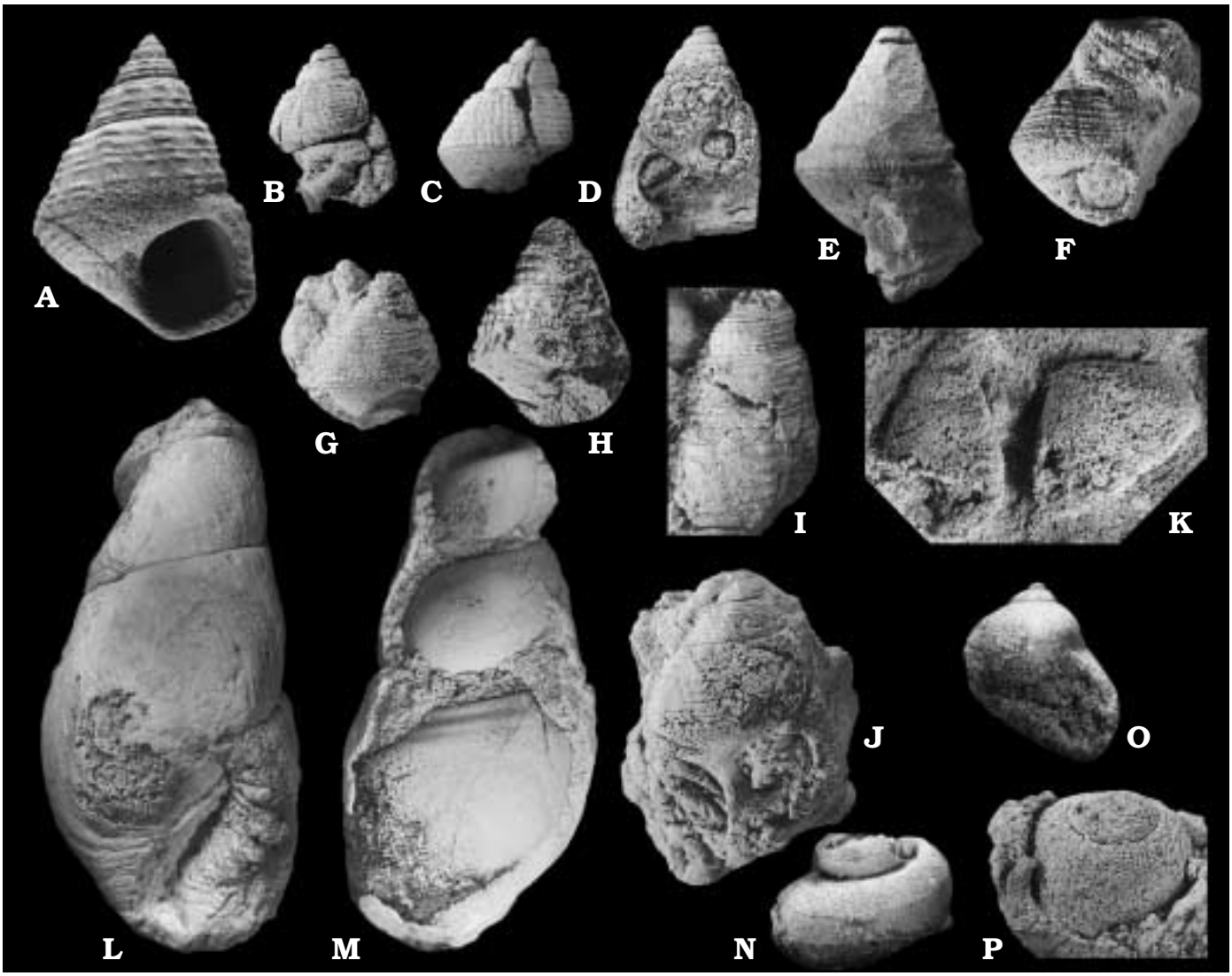

Fig. 8. *Kowalatrochus sanctacrucensis* association from the early and middle Frasnian of the upper Sitkówka Beds. **A–J**. *Kowalatrochus sanctacrucensis* gen. et sp. nov. **A**. Apertural view of shell, holotype GIUS 4-1569/Ko-81, × 2. **B**, **C**, **E–G**, **I**. Apertural and lateral views of shell with well preserved ornamentation. **B**, **C**. ZPAL Ga-VI/59. **E**. GIUS 4-1217/Ko-4. **F**. GIUS 4-1223/Ko-10. **G**. GIUS 4-1219/Ko-6. **I**. ZPAL Ga-VI/58. **B**, **C**, **E–G**. Natural size. **I**. × 1.5. **D**, **J**. Shells with poorly preserved last whorl, Jaźwica, set I, natural size. **D**. GIUS 4-1127/Jaź-22. **J**. GIUS 4-1120/Jaź-15. **H**. Shell with poorly preserved ornamentation, Grabina, set A, GIUS 4-1019/Gr-151, × 1.7. **K**. *Kowalatrochus* cf. *sanctacrucensis* gen. et sp. nov., lateral views, Sitkówka-Kowala, set B, GIUS 4-1214/SKo-10, × 2. **L**, **M**. *Westerna subcostata* (Schlotheim, 1820) comb. nov., Sitkówka-Kowala, set B, GIUS 4-851/SKo-6, natural size. **L**. Apertural view with well preserved ornamentation. **M**. Lateral view with shown palatal folds on internal mould. **N**. *Coelozone* sp., lateral view with wide selenizone, GIUS 4-1237/Ko-24, × 5. **O**. *Naticopsis* (*Naticopsis*) *inflata* (Roemer, 1843), apertural view of juvenile shell, GIUS 4-1238/Ko-25, × 6. **P**. *Naticopsis* (*Naticopsis*) *protogaea* (Goldfuss, 1844), lateral view of poorly preserved shell, GIUS 4-1353/Ko-75, × 2. **A–C**, **E–G**, **I**, **N–P**. Kowala, set A_2.

gradate with 5–6 whorls. Surface of the whorl flattened near suture and below strongly bent to form a weak, convex angulation. The ramp below this angulation is strongly inclined and becomes flattened on the narrowly phaneromphalous base. Rounded periphery at the border of the ramp and base. The selenizone is wide, flat and gently concaves, not bordered by spiral threads at the middle of the whorl ramp. Sutures are canaliculate. Aperture rounded.

Ornamentation consists of spiral cords at ramp and base, but in gerontic stage consist only of growth lines. Growth lines are orthocline near suture and become prosocline below with a small sinus at the ramp above the selenizone. Growth lines below selenizone are opisthocline. Protoconch unknown. Pleural angle is 82°.

Remarks.—This species has been described by Gürich (1896) on the basis of specimens from Kadzielnia. However, its illustration is absent in the Gürich's work. This is a relatively rare species, but a complete specimen has been found at the type locality. It has been designated as the neotype (GIUS 4-1478/Kad-3; Fig. 6F–H).

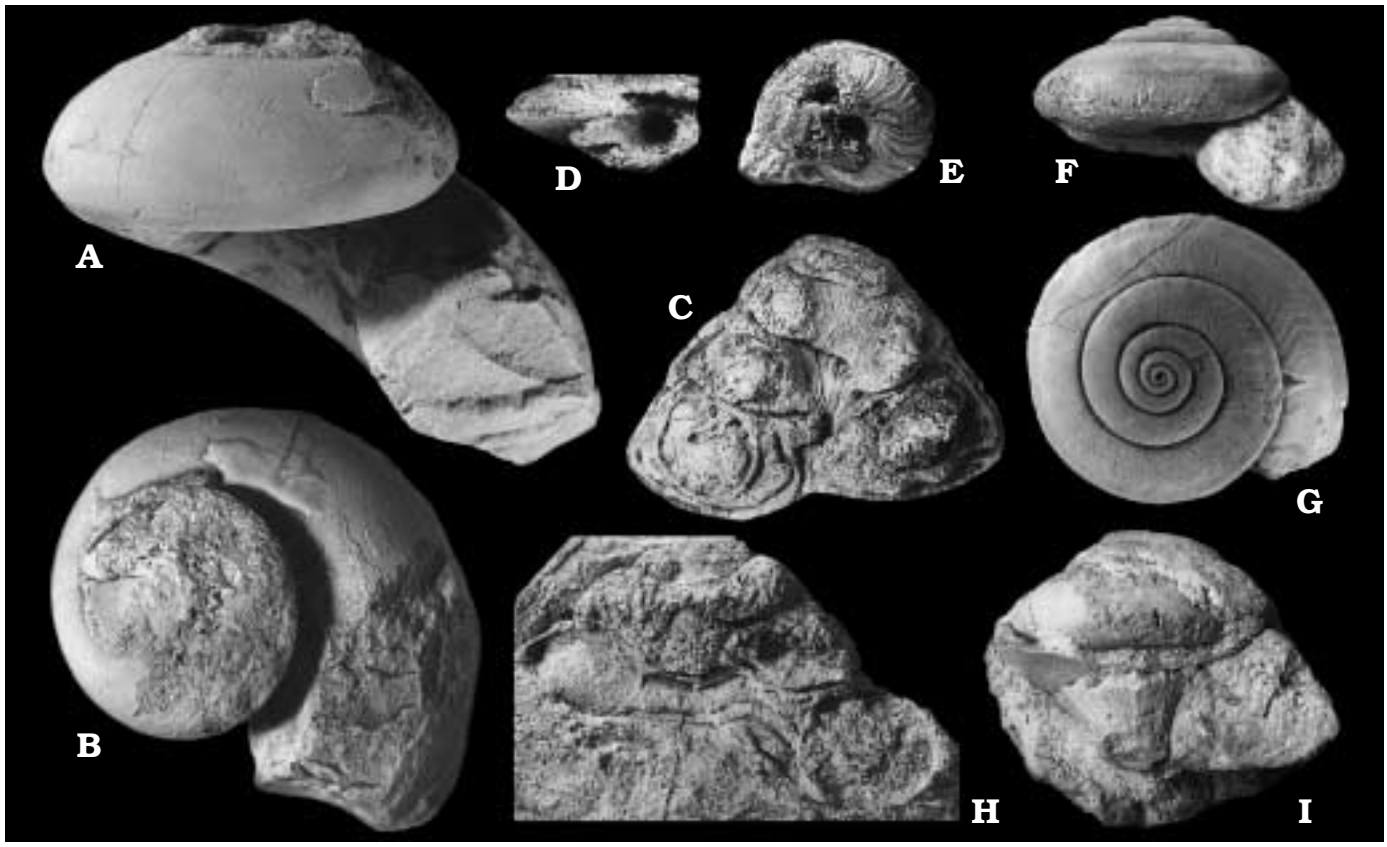

Fig. 9. *Orecopia kadzielniae* (Gürich, 1896) comb. nov. in *Kowalatrochus sanctacrucensis* association from lower and upper Sitkówka Beds (early and middle Frasnian). **A**, **B**. Apertural and apical view of internal mould with fragmentary preserved shell from the original Gürich's collection, Kadzielnia, set A, holotype MGUWr.1939.s. **C**. Axial section with visible funicles on umbilical wall, GIUS 4-1284/Gr-181. **D**, **E**. Apertural and basal view of shell with well preserved basal ornamentation, GIUS 4-1232/Ko-19. **F**, **G**. Apertural and apical view of shell with well preserved growth lines, GIUS 4-1041/Gr-173. **H**. Axial section with poorly preserved shell, GIUS 4-1045/Gr-177/1. **I**. Apertural view with fragmentary preserved shell, GIUS 4-1191/Gr-179. **A**–**C**, **F**–**I**. Grabina, set A; natural size. **D**, **E**. Kowala, set A_2, × 2.

Distribution.—Holy Cross Mountains: Kadzielnia, set A and Jaźwica, set J (the Kadzielnia Member, early Frasnian).

Superfamily Trochoidea Rafinesque, 1815
Family Holopeidae Wenz, 1938
Genus *Kowalatrochus* gen. nov.

Type species: *Kowalatrochus sanctacrucensis* gen. et sp. nov.

Type horizon and locality: Active quarry "Kowala" near Kielce, set A_2, the upper Sitkówka Beds, early Frasnian.

Derivation of the name: From type locality Kowala and *trochus* from trochiform shell.

Diagnosis.—*Kowalatrochus* gen. nov. differs from similar *Yunnania* Mansuy, 1912 by the shape of its shell. *Yunnania* has a turbiniform shell with an anomphalous base. *Compsonema* Gordon and Yochelson, 1983 has a narrow phaneromphalous base with a circumumbilical ridge. The relatively large trochiform shell and cryptomphalous base of *Kowalatrochus* distinguishes it from other representatives of the family Holopeidae (see Knight 1941; Knight et al. 1960; Gordon and Yochelson 1983). Protoconch unknown. Teleoconch has a stable ontogenic development.

Species assigned.—Only the type species.

Kowalatrochus sanctacrucensis sp. nov.

Fig. 8A–K.

Holotype: GIUS 4-1569/Ko-81 (Fig. 8A).

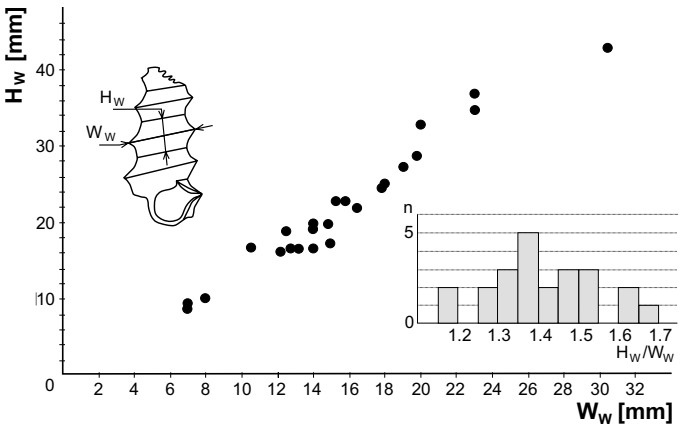

Fig. 10. Distribution of translation index (H_w/W_w) of *Loxoplocus* (*Donaldiella*) *karczewskii* sp. nov. from the late Frasnian of Panek (set B_3).

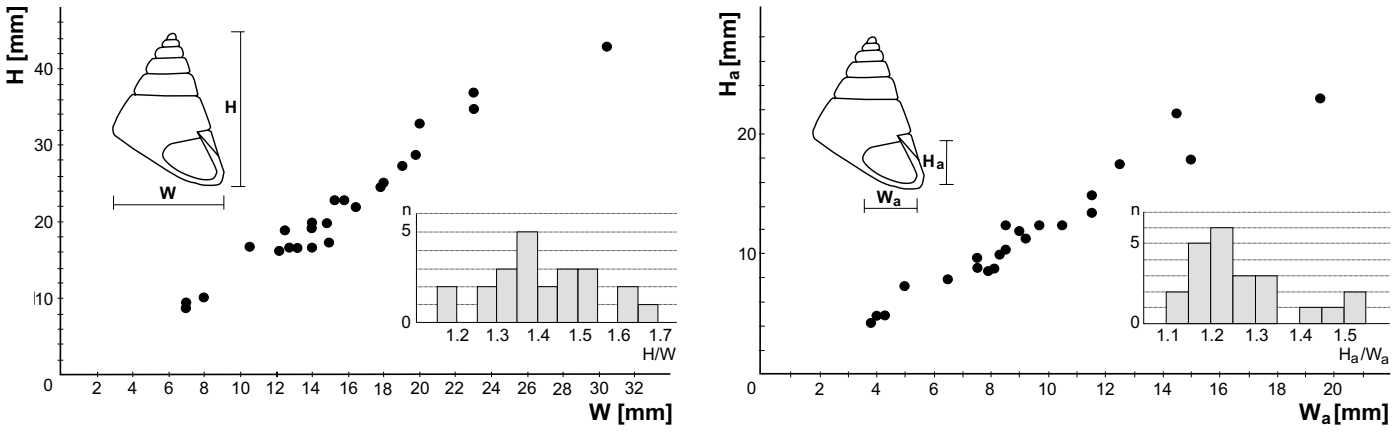

Fig. 11. Distribution of translation (H/W) and of apertural shape (H_a/W_a) indexes of *Kowalatrochus sanctacrucensis* gen. et sp. nov. from the early to middle Frasnian of the upper Sitkówka Beds.

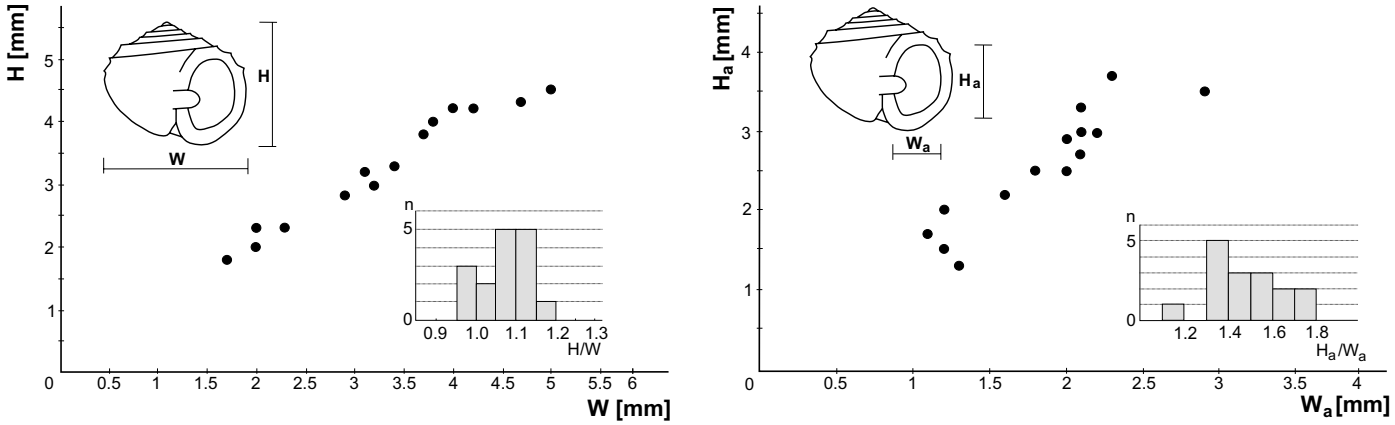

Fig. 12. Distribution of translation (H/W) and of apertural shape (H_a/W_a) indexes of *Grabinopsis guerichi* gen. et sp. nov. from the middle Frasnian of the upper Sitkówka Beds.

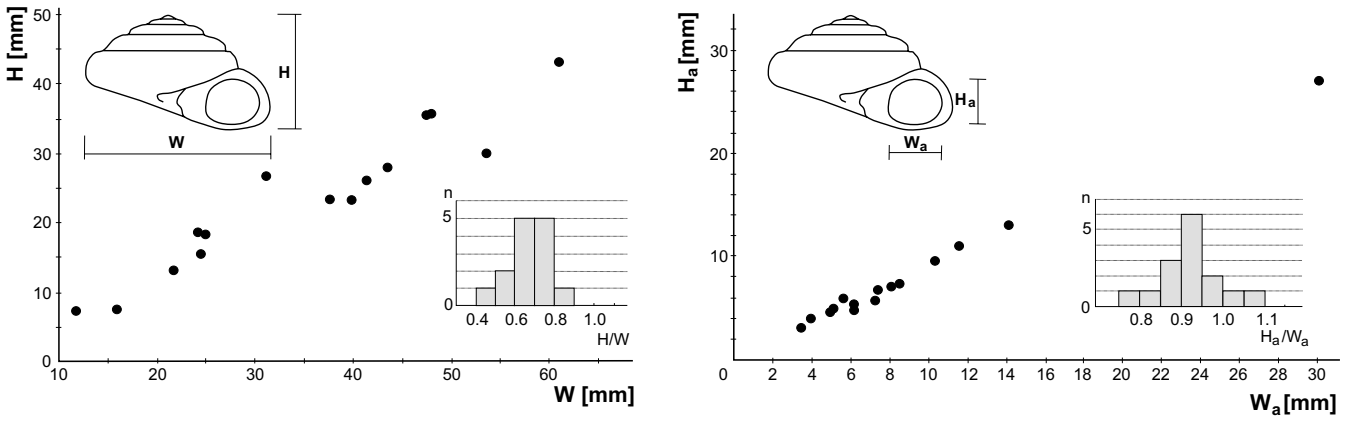

Fig. 13. Distribution of translation (H/W) and of apertural shape (H_a/W_a) indexes of *Orecopia kadzielniae* (Gürich, 1896) comb. nov. from the early and middle Frasnian of the upper Sitkówka Beds.

Type horizon and locality: As for the genus.

Derivation of name: From Latin name of the Holy Cross Mountains.

Material.—Thirty two almost completely preserved shells and about 60 fragments with well preserved ornamentation (ZPAL Ga-VI/49–55, 57–59; GIUS 4-1017/Gr-149, 4-1019–1020/Gr-151–152, 4-1022–1028/Gr-154–160, 4-1030–1034/Gr-162–166, 4-1045/Gr-177/2, 4-1115/Jaź-10, 4-1119–1128/Jaź-14–23, 4-1213–1214/SKo-9–10, 4-1217–1227/Ko-4–14, 4-1257–1258/Ko-44–45, 4-1336/Ko-58, 4-1348/Ko-70/8, 4-1351–1352/Ko-73–74).

Diagnosis.—Ornamentation consists of nine spiral cords on the whorl ramp and 10–11 spiral cords below the periphery

on the base. Wide collabral undulations are also visible on the ramp.

Description.—Large-sized shell (to 5 cm of height), trochiform with 7–8 whorls and thick walls of the spire. The height of the spire is a little larger than the height of the aperture. The ramps of the whorl are relatively sleeply sloping and weakly arched. A small callus is present on the cryptomphalous base. Small funicles surround the umbilicus. Sutures shallow, poorly demarcated. Aperture rounded, outer lip narrow along its edges. Protoconch is unknown. Pleural angle is stable (55–65°). Growth lines prosoclinal on the ramp and base. Ornamentation is mainly spiral: 9 spiral cords and 13–14 wide collabral undulations on the ramp of the whorl; the ninth spiral cord forms a prominent periphery; two strong spiral cords just below periphery, and the next 8–9 cords are weak. All spiral cords flattened and intersected by growth lines.

Variability.—The shells of *Kowalatrochus sanctacrucensis* show moderate differences of the translation index H/W (1.15–1.65) and the index of apertural shape H_a/W_a (1.1–1.5) (Fig. 11).

Distribution.—Holy Cross Mountains: Kowala, set A_2, Jaźwica, set I–K, and ?Sitkówka-Kowala, set B (the upper Sitkówka Beds; early Frasnian); Grabina, set A (the upper Sitkówka Beds; middle Frasnian).

Superfamily Neritoidea Rafinesque, 1815
Family ?Plagiothyridae Knight, 1956
Genus *Grabinopsis* gen. nov.

Type species: *Grabinopsis guerichi* sp. nov.

Type horizon and locality: the inactive quarry "Grabina" (W part of Kielce), set B, the upper Sitkówka Beds, middle Frasnian.

Derivation of the name: from type locality, Grabina.

Diagnosis.—*Grabinopsis* gen. nov. is charakterized by a rounded small shell with a low spire. Columallar lip with one prominent columellar fold. Ornamentation contains of two spiral angular ridges just below the suture. *Grabinopsis* gen. nov. differs from *Dirachis* Whidborne, 1891 by its lower spire and the single columellar fold. Other genera from the family Plagiothyridae (*Plagiothyra* Whidborne, 1892 and *Littorinides* Knight, 1937) have much higher turbiniform shells, anomphalous bases, and more developed spiral ornamentation. The almost sphaerical shell is similar to the shell of *Naticopsis* M'Coy, 1844 but the last whorl of *Grabinopsis* has a higher an aperture as well as aperture expanded in a direction perpendicular to the axis of the shell. *Grabinopsis* has a minutely phaneromphalous base and a spiral ornamentation not known in *Naticopsis*.

Remarks.—The naticiform shell, the presence of spiral ridges, and the prominent columellar fold suggest affinities with the family Plagiothyridae. However, some doubts are raised because of the absence of a well preserved last whorl, growth lines, and due to unknown nature of the protoconch.

Species assigned.—Only the type species.

Grabinopsis guerichi sp. nov.

Fig. 5A–F.

Genus? sp.; Gürich 1896: 311, pl. 11: 4.

Holotype: GIUS 4-981/Gr-113 (Fig. 5A).

Type horizon and locality: As for the genus.

Derivation of the name: In memory of Dr. Georg Gürich who found first specimens of this gastropod.

Material.—Eighteen almost complete shells and 9 fragments (GIUS 4-974–981/Gr-106–113, 4-1207/SzG-12/2).

Diagnosis.—The spire has deep and nearly canaliculate sutures. Ornamentation consists of two spiral ridges on the upper part of the whorl.

Description.—Small-sized naticiform shell (maximum height 4 mm), with a low spire and having 5–6 whorls. Whorls strongly embrace one another. Profile of the last whorl is rounded with a weak angulation formed by a prominent spiral ridge in the upper part of the labrum. A second weak spiral ridge runs just below the first one. Surfaces between the suture and first ridge, as well as between the spiral ridges, are slightly concave. Sutures are deep and nearly canaliculate. Whorls join just below the lower weak spiral ridge.

Base rounded, narrowly phaneromphalous. Umbilicus surrounded by a ridge which is formed at the contact of outer lip with the basal wall. A very prominent columellar fold present at the middle of the columellar lip. There is a distinct concave notch below the columellar fold. Aperture is hemispherical. Lower part of the labrum is elongated. Ornamentation consists of two spiral ridges on the upper part of the whorl. Growth lines and protoconch are unknown. Pleural angle is stable (100–135°).

Variability.—Shells of *Grabinopsis guerichi* gen. et sp. nov. is characterized by few changes of the relative shell height as well as by a more variable apertural shape (Fig. 12).

Remarks.—The first shells of this species were found by Gürich in Frasnian limestones at Karczówka hill. However, these shells had not been determined because of their poorly preserved character. Specimens from the original Gürich's collection have been lost.

Distribution.—Holy Cross Mountains: Szczukowskie Górki, Grabina, set B (the upper Sitkówka Beds; middle Frasnian).

Suborder uncertain
Family Omphalotrochidae Knight, 1945
Genus *Orecopia* Knight, 1945

Type species: *Orecopia mccoyi* (Walcott, 1884); Frasnian, North America.

Remarks.—Genus *Orecopia* Knight, 1945 is characterized by a trochiform, narrowly phaneromphalous shells with a wide rounded sinus on the upper part of the labrum. The similar genus *Omphalotrochus* Meek, 1864 has a spiral ridge at the upper part of outer lip. *Labrocuspis* Heidecker, 1959 differs from *Orecopia* by its cryptomphalous base with a wide callus. *Orecopia* displays an archaeogastropod-type proto-

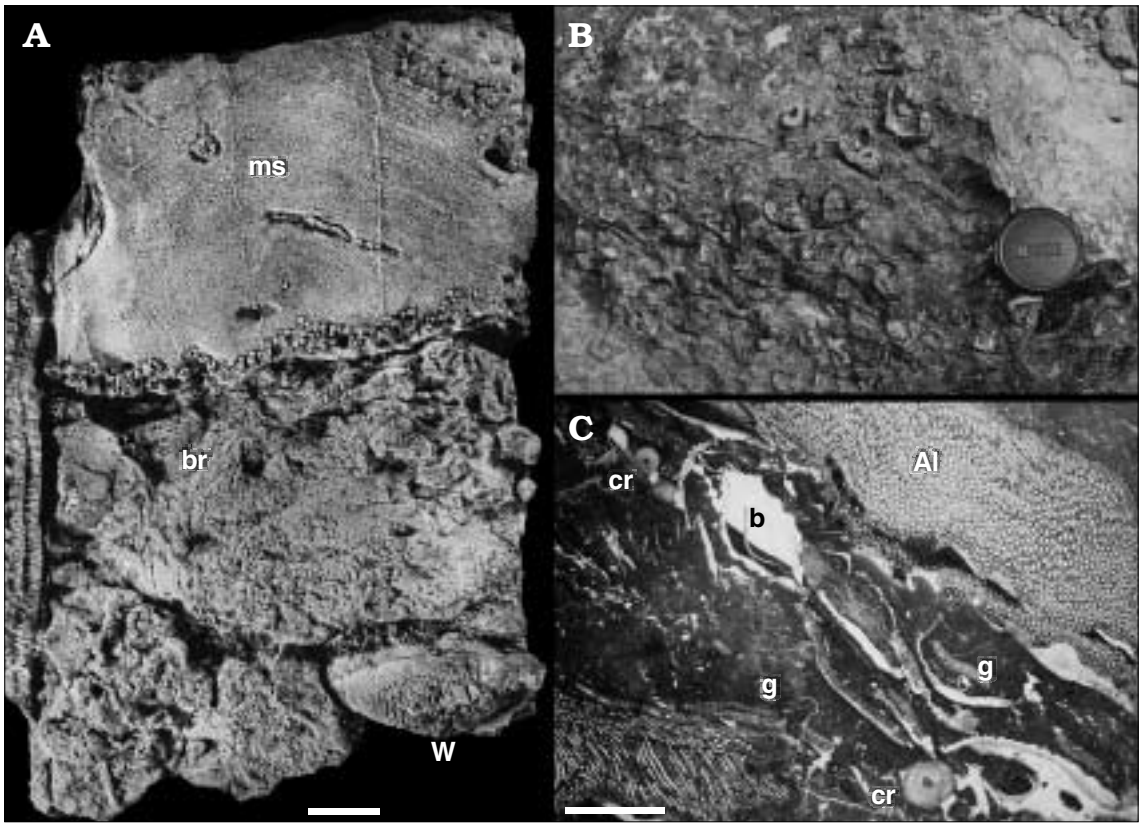

Fig. 14. Reef limestones containing gastropod fauna from early and middle Frasnian of Kowala. **A**. Stromatoporoid-coral packestone-floatstone with massive stromatoporoids (ms), branched rugosans (br), and large thick-shell gastropods *Westerna subcostata* (Schlotheim, 1820) comb. nov. (W), set A_2, GIUS 4-1349/Ko-71. **B**. Nest concentrations of *Kowalatrochus sanctacrucensis* gen. et sp. nov. shells in wackstone-packestone, west wall of the quarry, set A_2. **C**. *Alveolites* (Al) bindstone with brachiopods (b), crinoids (cr), and gastropods (g), set C, GIUS 4-1509/Ko-80. Scale bars 1cm.

conch and cyrtoconoid teleoconch. Older whorls are sometime closed by septa.

Orecopia kadzielniae (Gürich, 1896) comb. nov.

Fig. 9A–I.

Pleurotomaria kadzielniae sp. nov.; Gürich 1896: 306, pl. 11: 3.

Straparollus (*Straparollus*) *grabinensis* sp. nov.; Karczewski 1989: 110, pl. 3: 1.

Holotype: MGUWr.1939.s (Fig 9A, B).

Type horizon and locality: Inactive quarry "Kadzielnia" (S part of Kielce), set A, the Kadzielnia Member, early Frasnian.

Material.—Seven almost complete specimens, 3 internal moulds, 1 well preserved base as well as 6 fragments of the spire and 7 axial sections (M.G.U.Wr. 1939.s.; ZPAL Ga-VI/14, 16–22; GIUS 4-1021/Gr-153, 4-1024/Gr-156/2, 4-1028/Gr-160/2, 4-1036/Gr-168, 4-1038–1043/Gr-170–175, 4-1045/Gr-177/1, 4-1046/Gr-178, 4-1191/Gr-179, 4-1232/Ko-19, 4-1284/Gr-181).

Diagnosis.—*Orecopia kadzielniae* differs from *O. mccoyi* (Walcott, 1884) by narrowly phaneromphalous base. *O. cotei* Pedder, 1966 has a carina at the periphery of the whorl. *O. kirchholmiensis* (Keyserling, 1846) has more rounded whorls and deeper sutures (see Chernychev 1884, 1887).

Description.—Large, high to low trochiform shell (maximum width 6.5 cm) with 6–7 whorls. First two whorls are flattened, next one abuts just below rounded periphery. Sutures are relatively flat. Ramp of the whorl is almost flat from suture to about half of the distance between suture and periphery. Wide sinus developed on the flat part of the ramp. Lower part of the ramp has a concave spiral belt with a breath equal to about ¼ of ramp width. Base is rounded, narrowly phaneromphalous. Columellar lip is strongly thickened. Umbilicus deep, surrouded by thick funicles. Growth lines form a wide, insignificant sinus on the base. Abandoned whorls are closed by septa (see Fig. 16A). Aperture rounded, protoconch and outer lip are not preserved. Pleural angle decreasing during ontogenic development from 100 to 170°.

Variability.—The population of the species *O. kadzielniae* shows sufficiently high variability of the translation index H/W (0.45–0.85). It is caused by changes of the spire height and the relatively stable values of the apertural shape index H_a/W_a (Fig. 13).

Remarks.—This species was described by Gürich (1896) from the Frasnian of Kadzielnia. The holotype of *Pleurotomaria kadzielniae* is an internal mould and it is housed in Gürich's collection at the Geological Museum of Wrocław University. The concave belt at the ramp of the whorl had been identified as a selenizone in the original description.

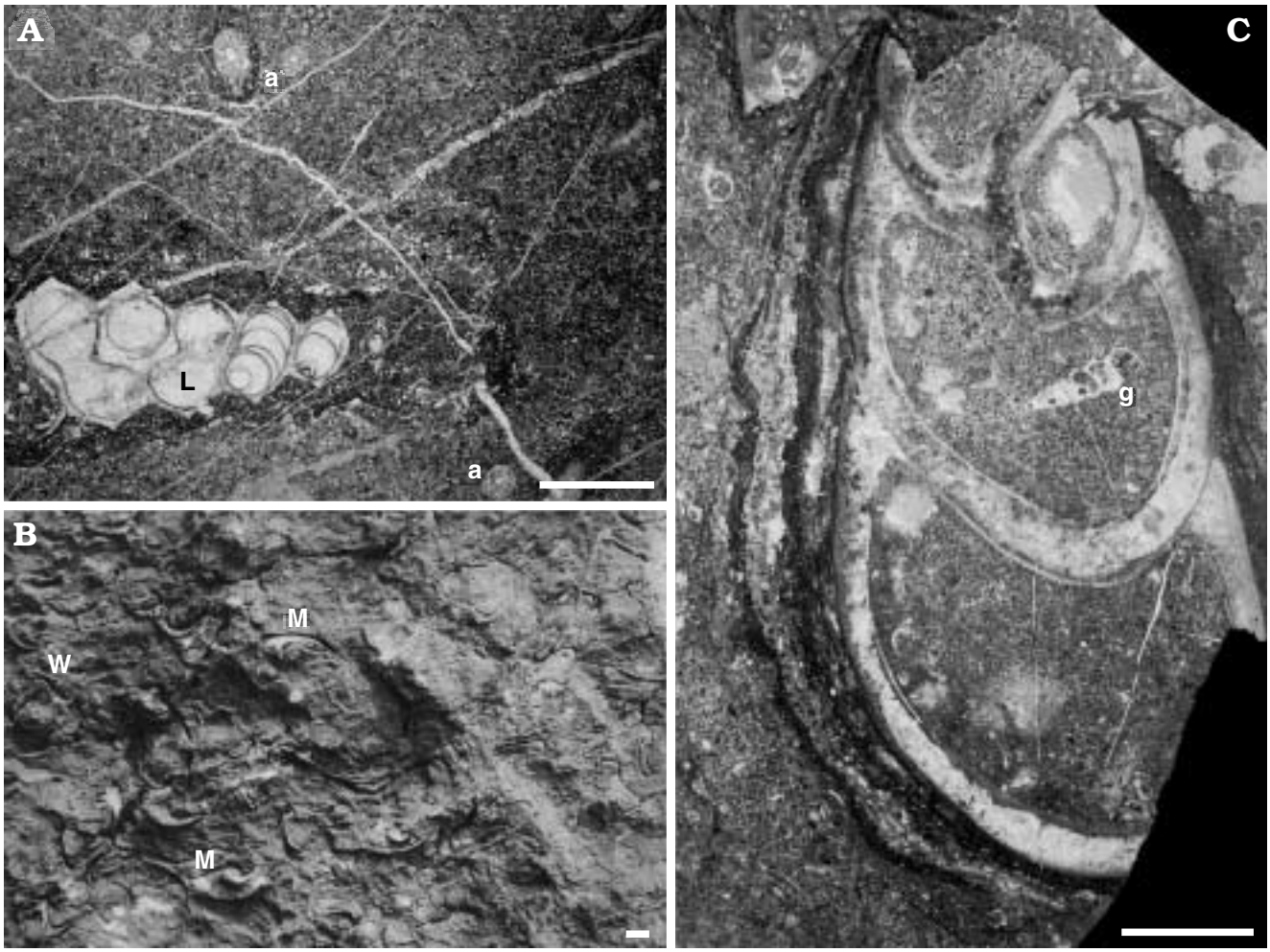

Fig. 15. Late Frasnian limestones of the Detrital-Stromatoporoid Beds at Panek. **A**. Lagoonal wackestone with amphiporoids (a) and *Loxoplocus* (*Donaldiella*) *karczewskii* sp. nov. (L) with septation of spire, set B_3, GIUS 4-1515/Pan-85. **B**. Reefal packstone-rudstone with the bivalve *Megalodon* sp. (M) and the gastropod *Westerna subcostata* (Schlotheim, 1820) comb. nov. (W), set B_2. **C**. Oncoidal packstone with the thick-shell gastropod *Westerna subcostata* (Schlotheim, 1820) comb. nov., as oncoid nodule, and other unidentified gastropods (g), set B_2, GIUS 4-1514/Pan-84. Scale bars 1 cm.

Shape and biometrical measures clearly indicate the resemblance of Gürich's specimen to the specimens collected by the author at Grabina. That allows revision of this species.

Distribution.—Holy Cross Mountains: Kadzielnia, set A (the Kadzielnia Member), Kowala, set A_2 and Grabina, set A (the upper Sitkówka Beds; from early to middle Frasnian).

Frasnian gastropod faunas from the Kowala Formation

An *assemblage* is defined as a community of various organic group taxa, living in the same environment, with prominent role of gastropods. An *association* is defined as part of an assemblage containing only one organic group. All these synecological units are linked with facies types described by Racki (1993b) for Frasnian faunal assemblages. Five associations of gastropods and one assemblage were analysed in the context of field observations, microfacies, and acompanying fauna (Fig. 2).

Lagoonal habitats

***Loxoplocus* (*Donaldiella*) *karczewskii* Assemblage**.—Typical site: the "Panek" quarry, set B_3 (Detrital-Stromatoporoid Beds; late Frasnian). The biota is connected with the light gray wackestone and packstone (facies L-1; Fig. 15A), containing amphiporoids, massive stromatoporoids and calcispheres. The uncommon species *Loxoplocus* (*Donaldiella*) *karczewskii* (Table 1) and also the very rare unidentified pleurotomarids are the dominant macrofaunal taxa. Those molluscs lived in the calm, shallow waters of back-reef and lagoon (Fig. 17C).

Reef habitats

***Euryzone kielcensis* Association** of the Kadzielnia-type Assemblage (Fig. 7).—Typical site: Kadzielnia, set A (the Kadzielnia Member; early–middle Frasnian). Other locations:

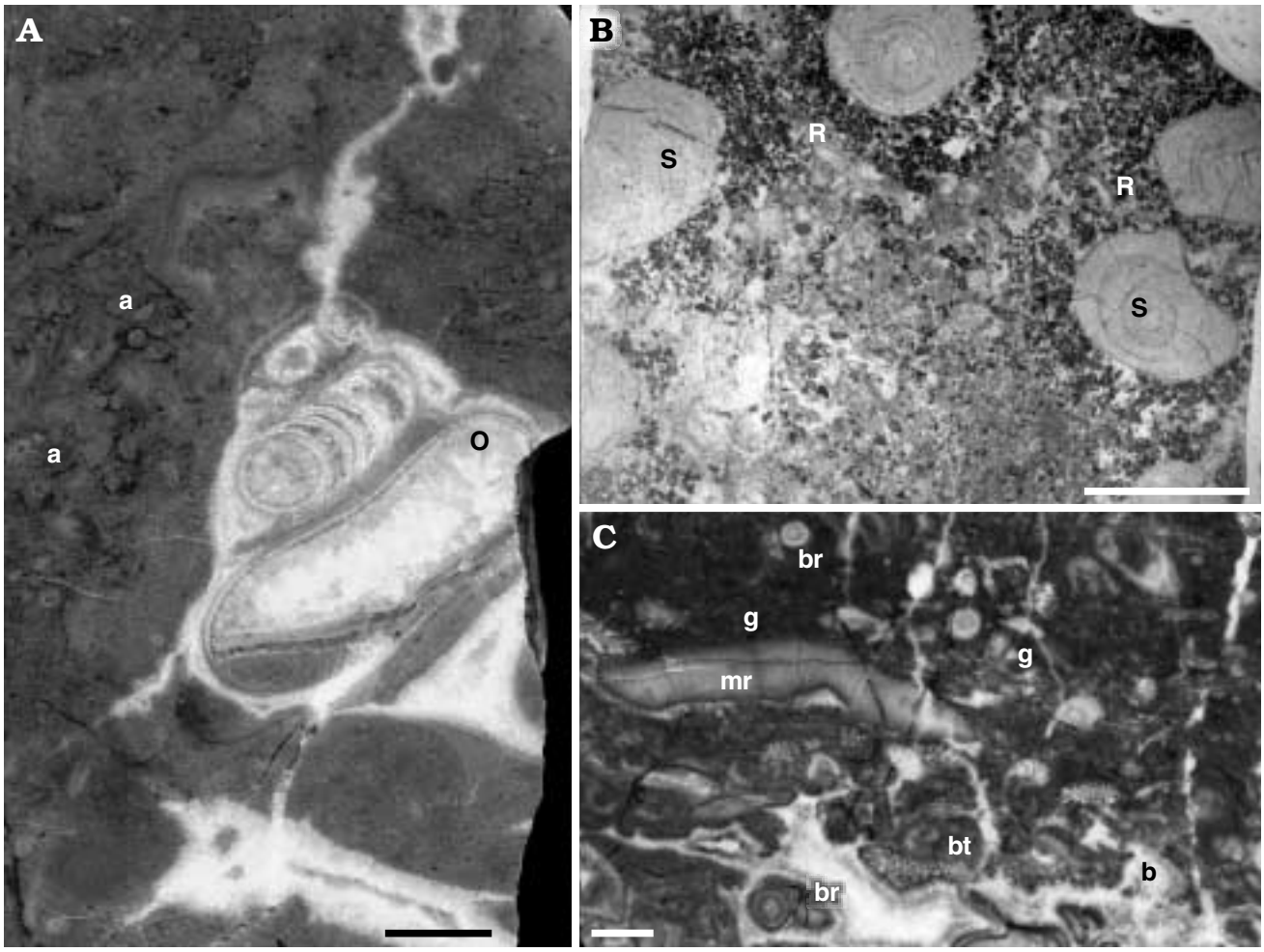

Fig. 16. Middle and late Frasnian limestones of the upper Sitkówka Beds and of the Detrital Beds from Grabina. **A**. Stromatoporoid-coral floatstone with amphiporoids (a) and the large gastropod *Orecopia kadzielniae* (Gürich, 1896) comb. nov. (O). Geopetal structure in the last whorl of shell and septation of the spire are visible, GIUS 4-1510/Gr-182, set A. **B**. *Stachyodes* (S)–*Renalcis* (R) bafflestone from a giant colony, set B, GIUS 4-1511/Gr-183. **C**. Coral rudstone with massive (mr) and branched (br) rugosans, branched tabulates (bt), brachiopods (b), and gastropods (g), set C, GIUS 4-1512/Gr-184. Scale bars 1 cm.

Jaźwica (set J), Kowala (set C). The Kadzielnia-type Assemblage, representing the very diverse biocoenosis of mud mounds, has been derived from the stromatoporoid bindstone (facies R-3b; Fig. 14C). Mud mounds were created below the wave base. The community contains (Fig. 17A; Kaźmierczak 1971; Szulczewski 1971; Szulczewski and Racki 1981): massive stromatoporoids, massive and branched tabulates, branched and solitary rugosans (the *Macgeea–Thamnophyllum* Assemblage; Wrzołek 1988, 1993), brachiopods (the *Fitzroyella alata–Parapugnax breccie* Association; Racki 1993a), trilobites (Chlupač 1993), ostracods (Malec and Racki 1993), crinoids (the *Schyschcatocrinus* Assemblage; Głuchowski 1993), echinoids, calcisponges (Hurcewicz 1993), tentaculites (Hajłasz 1993) and microproblematics: moravamminids and labyrintoconids (Racki and Soboń-Podgórska 1993). The rich association contains at least 11 taxa of gastropods (see Table 1): *Euryzone kielcensis*, *Westerna subcostata*, *Naticopsis* (*Naticopsis*) *inflata*, *Spanionema scalaroides*, *Orecopia kadzielniae*, *Roemeriella octocincta*, *Porcellia bifida*, *Villmaria ventricosa*, as well as unidentified murchisonids and holopeids.

***Kowalatrochus sanctacrucensis* Association** of the *Actinostroma* Assemblage (Figs. 8, 17A, B).—Typical site: the "Kowala" quarry, set A (Fig. 3; the upper Sitkówka Beds; early Frasnian). Other locations: Jaźwica (set I), Sitkówka-Kowala (set B), Grabina (set A). The association is present in floatstones and rudstones, characteristic for the early Frasnian reef environment (facies R-3fr or R-3r; Figs. 14A, B, 16A). Fauna in those environments are comprised mostly of massive and branched stromatoporoids (the *Actinostroma* Assemblage; Racki 1993b) and tabulates, branched rugosans, and less often massive rugosans (*Macgeea–Thamnophyllum* and *Hexagonaria hexagona* Assemblages; Wrzołek 1988, 1993), brachiopods (*Desquamatia macroumbonata* association; Racki 1993a), calcisponges (Hurcewicz 1993), crinoids (the *Schyschcatocrinus* Assemblage; Głuchowski 1993), issinellids and calcispheres (see Racki and Soboń-Podgórska 1993), and ostracods (Fig. 17A, B). The associa-

tion consists of: *Kowalatrochus sanctacrucensis*, *Westerna subcostata*, *Orecopia kadzielniae*, *Coelozone* sp., *Straparollus* (*Straparollus*) *serpens*, *Naticopsis* (*Naticopsis*) *inflata*, *Naticopsis* (*Naticopsis*) *protogaea*, and *Lahnospira taeniata* (see Table 1).

***Straparollus* (*Straparollus*) *circularis* Associaion** of the *Actinostroma* Assemblage (Fig. 4).—Typical site: the "Panek" quarry, set B_2 (Fig. 3; the Detrital-Stromatoporoid Beds, late Frasnian). Other locations: Sitkówka-Jaźwica (set B). The association occurs in stromatoporoid-coral rudstones (facies R-3r; Fig. 15B, C). It is associated with stromatoporoids, tabulates, as well as massive and branched rugosans (the *Frechastraea smithi* Assemblage; Wrzołek 1988, 1993), thick-shell bivalves of the genus *Megalodon* (see Fig. 15B; Karczewski 1992), and rarer brachiopods and crinoids (the *Calleocrinus* Assemblage; Głuchowski 1993). There are also diverse microbiotas: solenoporids, chlorophytes (?*Jansaella*), foraminifers *Nanicella, Eodonosaria* (Racki and Soboń-Podgórska 1993), ostracods (Malec and Racki 1993) and calcispheres (Fig. 17C). Among the gastropods, the association contains: *Straparollus* (*Straparollus*) *circularis*, *Westerna subcostata* and unidentified murchisonids (see Table 1).

***Grabinopsis guerichi* Association** of the *Stachyodes* Assemblage (Fig. 5).—Typical site: Grabina, set B (Fig. 3; the upper Sitkówka Beds; middle Frasnian). The association is derived from the *Stachyodes–Renalcis* buildup with a wackestone matrix (facies R-2b; Fig. 16B). There are large fragments of crinoid columns and sometimes even complete preserved calices of crinoids (the *Calleocrinus* Assemblage; Głuchowski 1993), numerous ostracods, tiny brachiopods, and bellerophontid gastropods dispersed among the branches of the giant *Stachyodes* and *Renalcis* buildup (Fig. 17Ba). This gastropod fauna includes: *Grabinopsis guerichi*, *Naticopsis* (*Naticopsis*) *inflata*, *Palaeozygopleura* (*Rhenozyga*) sp. A, *Palaeozygopleura* (*Rhenozyga*) cf. *retrostriata*, *Roemeriella cyclostomoides*, *Villmaria ventricosa*, *Murchisonia* (*Murchisonia*) *nerinea*, *Liospira* sp., as well as unidentified loxonemids and subulitids (see Table 1).

***Naticopsis* (*Naticopsis*) *excentrica* Association** of the *Frechastraea pentagona* Assemblage (Fig. 4).—Typical site: Grabina, set C (Fig. 3; the Detrital Beds; late Frasnian). The association is linked with rudstone (facies R-1; Fig. 16C) built with fragments of reef-building organisms: massive stromatoporoids, tabulates, massive and branched rugosans (the *Frechastraea pentagona* Assemblage; Wrzołek 1988), and also brachiopods, remains of crinoids (the *Calleocrinus* Assemblage; Głuchowski 1993), plates of echinoids and ophiuroids, nautiloids, bivalves, bellerophonts, fish remains, and fragments of trilobites (see Coen-Aubert and Wrzołek 1991) (Fig. 17B). The strongly diversified association consists of following taxa (see Table 1): *Straparollus* (*Straparollus*) *serpens*, *Liospira* sp., *Villmaria ventricosa*, *Lahnospira taeniata*, *Roemeriella octocincta*, *Porcellia bifida*, *Naticopsis* (*Naticopsis*) *inflata*, *Naticopsis* (*Naticopsis*) *excentrica*, *Naticopsis* (*Naticopsis*) *protogaea*, *Palaeozygopleura* (*Rhenozyga*) sp. A, *Palaeozygopleura* (*Rhenozyga*) sp. B and undetermined microdomatids, murchisonids and loxonematids.

Synecological interpretation

There are a couple of widespread eurytopic gastropod species among the recognized groups and associations, for example: *Naticopsis* (*Naticopsis*) *inflata*, *Roemeriella octocincta*, *Villmaria ventricosa*, *Macrochilina ventricosa*, and *Palaeozygopleura* (*Rhenozyga*) cf. *retrostriata*. Sometimes they are known from different environments (reef or open shelf). There are also some stenotypic species connected only with a specific type of habitat, for example: *Kowalatrochus sanctacrucensis*, *Grabinopsis guerichi*, *Euryzone kielcensis*.

The gastropod associations of the lagoonal facies are quite typical. The dominant element among them is the turriculate species *Loxoplocus* (*Donaldiella*) *karczewskii.* It is very hard to find any specimens with discoidal shells among this association. Turriculate shells could be adapted for life among the branched corals or stromatoporoids, which often dominated this environment (Fig. 16C).

There are numerous large thick-shell gastropods in the reef associations, exemplified by *Kowalatrochus sanctacrucensis*, *Westerna subcostata*, and *Orecopia kadzielniae*, adapted for existence in high energy conditions (Fig. 17A–C). A separate group is an association with small, thin-shelled gastropods, often dwelled (?) in the reef slots and among the colonies of the reef-building organisms (Fig. $17B_2$). Possibly, they used the protective function of the colonial skeletons against enemies or strong waving, e.g., *Palaeozygopleura* (*Rhenozyga*) sp., *Grabinopsis guerichi* gen. et sp. nov., *Spanionema scalaroides* (Whidborne, 1889). The similar taxa to gastropods from the *Grabinopsis guerichi* and *Naticopsis* (*Naticopsis*) *excentrica* associations (i.e., *Straparollus*, *Murchisonia*, *Loxonema*) also exist in Frasnian reef facies of Western Canada (see Leavitt 1968). Similar ecologi-

Fig. 17. Reconstructions of macrobenthic assemblages of the Frasnian Dyminy reef complex. **A**. Early and middle Frasnian environments of the Southern Kielce Region (Kowala; after Racki 1993a). **B_1**. Middle and late Frasnian environments of the Northern Kielce Region (Grabina). **B_2**. Habitat of small gastropods among branches of *Stachyodes–Renalcis* buildups. **C**. Late Frasnian environments of the Central Kielce Region (Panek); a, *Amphipora*; s, *Stachyodes*; ms, massive stromatoporoids; al, *Alveolites*; sy, syringoporids; bt, branched tabulates; rugosans: mr, massive, br, branched, sr, singular; sp, sponges; rc, receptaculids; b, brachiopods; rh, rhynchonellids; gastropods: St, *Straparollus*; W, *Westerna*; O, *Orecopia*; L, *Loxoplocus*; g, other gastropods; p, bivalves; M, *Megalodon*; n, nautiloids; t, trilobites; os, ostracods; cr, crinoids; e, echinoids; f, fishes; R, *Renalcis*; S–R, *Stachyodes–Renalcis* buildups; mm, microbial mats. →

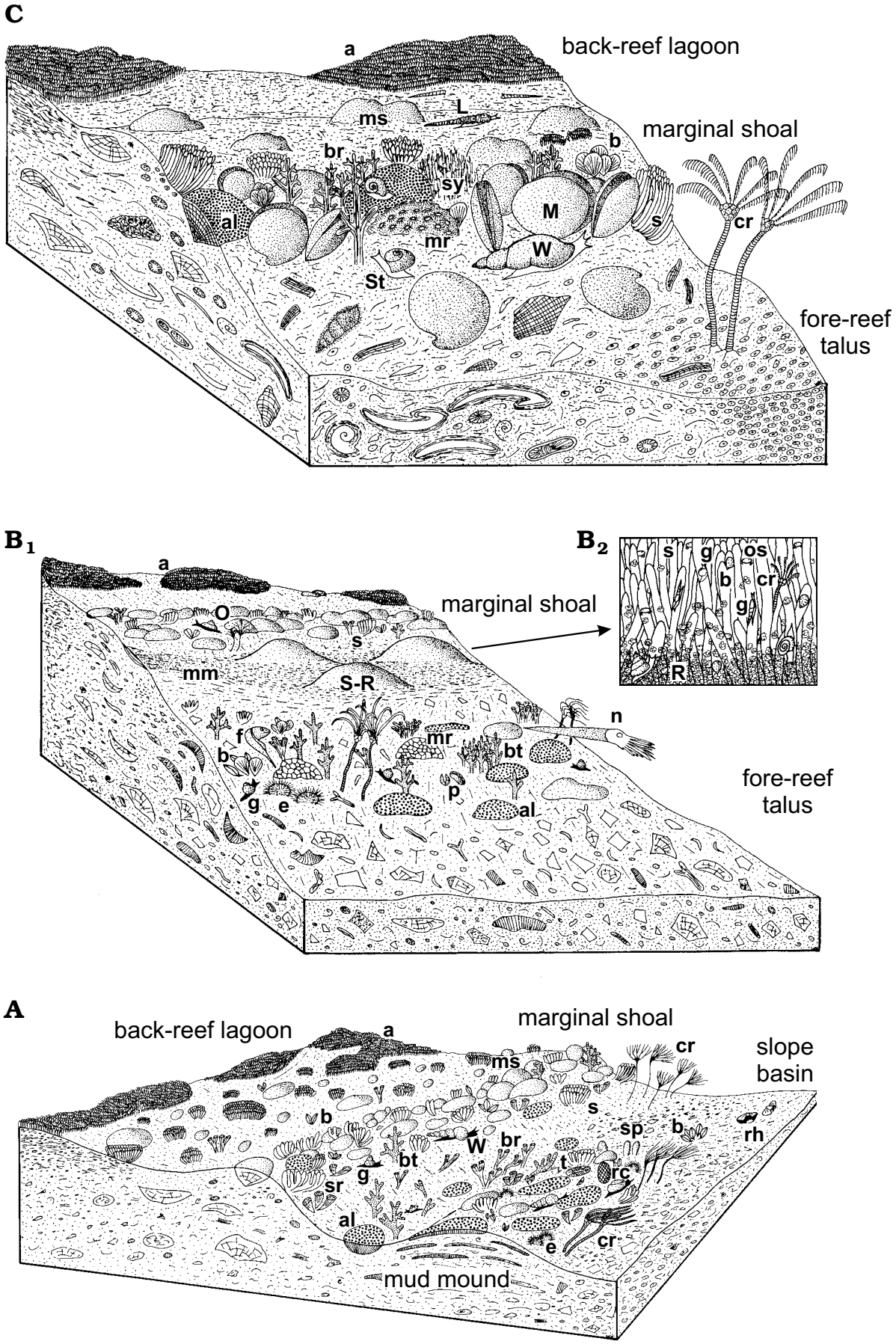
C
a
back-reef lagoon
ms
L
marginal shoal
br
b
sy
M
al
s
cr
mr
W
St
fore-reef
talus
B1
B2
a
marginal shoal
s
g
os
b
cr
g
O
s
mm
S-R
R
n
f
mr
bt
b
g
e
p
al
fore-reef
talus
A
back-reef lagoon
a
marginal shoal
cr
slope
basin
ms
s
b
sp
b
rh
W
br
bt
t
g
rc
sr
al
e
cr
mud mound

Table 1. Occurrence of Frasnian gastropods in the Holy Cross Mountains (after Krawczyński 1998, 1999); l, lower, u, upper.

Geochronology	Frasnian										
	early			middle						late	
Conodont biozones (Ziegler and Sandberg 1990)	*Pa. falsiovalis*		*Pa. transitans*	*Pa. punctata*	*Pa. hassi*		*Pa. jamieae*	*Pa. rhenana*			*Pa. linguiformis*
	l	u			l	u		l	u		
Sea-level cycles (Johnson *et al.* 1985)	IIb		IIb/c	IIc						IId	
Regional shallowing-upward cycles (Racki 1993b, 1997)	G/F-III		IC	F-I						F-II	
Euomphaloidea											
Straparollus (S.) serpens (Phillips, 1841)				■	■	■	■	■	■	■	■
Straparollus (S.) circularis (Phillips, 1841)			■	■	■	■	■	■	■	■	■
Pleurotomarioidea											
Liospira sp.										■	■
Villmaria ventricosa Heidelberger, 2001	■	■	■					■	■	■	■
Lahnospira taeniata (Sandberger, 1842)			■	■	■	■	■	■	■	■	■
Loxoplocus (Donaldiella) karczewskii sp. nov.										■	■
Euryzone kielcensis (Gürich, 1896)			■								
Coelozone sp.	■	■									
Trochoidea											
Kowalatrochus sanctacrucensis gen. et sp. nov.	■	■		■	■	■	■	■	■		
Roemeriella octocincta (Roemer, 1843)			■	■	■	■	■	■	■	■	■
Roemeriella cyclostomoides (Roemer, 1850)								■	■		
Cirroidea											
Porcellia bifida (Sandberger & Sandberger, 1850–1855)			■							■	■
Murchisonioidea											
Murchisonia nerinea (Sandberger & Sandberger, 1850–1855)								■	■	■	■
Murchisonia sp.			■								
Omphalotrochidae											
Orecopia kadzielniae (Gürich, 1896)	■	■		■	■	■	■	■	■		
Neritoidea											
Grabinopsis guerichi gen. et sp. nov.				■	■	■	■	■	■		
Naticopsis (N.) inflata (Roemer, 1843)	■	■	■	■	■	■	■	■	■	■	■
Naticopsis (N.) protogaea (Goldfuss, 1844)	■	■								■	■
Naticopsis (N.) excentrica (Roemer, 1843)										■	■
Loxonematoidea											
Palaeozygopleura (Rhenozyga) cf. *retrostriata* (Kirchner, 1915)								■	■	■	■
Palaeozygopleura (Rhenozyga) sp. A	■	■	■	■	■	■	■	■	■		
Palaeozygopleura (Rhenozyga) sp. B								■	■	■	■
Spanionema scalaroides (Whidborne, 1889)			■	■	■	■	■	■	■		
gen. et sp. ex fam. Loxonematidae indet.				■	■	■	■	■	■	■	■
Subulitoidea											
Macrochilina ventricosa (Goldfuss, 1844)				■	■	■	■	■	■	■	■
Westerna subcostata (Schlotheim, 1820)	■	■	■	■	■	■	■	■	■	■	■
gen. et sp. ex fam. Subulitidae indet.								■			

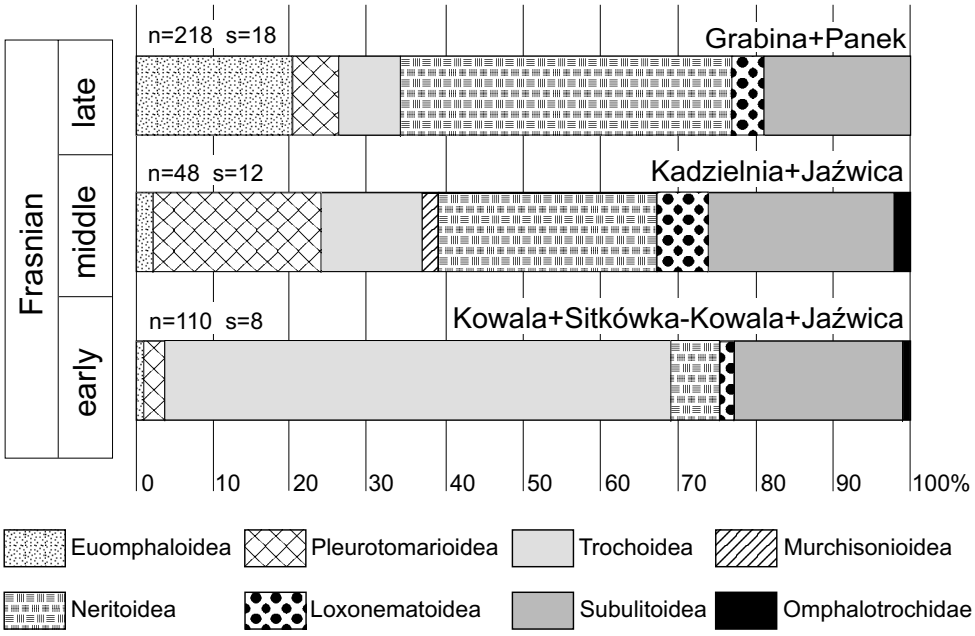

Fig. 18. Frasnian taxonomic composition changes of gastropod associations from the Holy Cross Mountains (after Krawczyński 1998).

cal differentiation into large- and small-sized groups have been observed in Kadzielnia-type brachiopods (Szulczewski and Racki 1981). Gastropods are a group that existed in each type of habitat of the Devonian shelf. They showed very high tolerance to changes in salinity, temperature and water depth (Murray 1966; Jamieson 1971). In the Frasnian carbonate complex of the Holy Cross Mountains, the huge majority of reef habitat associations (i.e., five associations) over the groups of lagoonal habitat (only one) was stated (Fig. 2). A similar synecological differentiation is observed in the Givetian reef complex of the North-East Australia (Cook 1995) as well as Frasnian reef complexes of the West Australia (Playford 1980), and Canada (Murray 1966). Slightly different patterns of gastropod associations are observed in Givetian reefs of Western Canada, where uncommon specimens can be found equally in all facies (Vopni and Lerbekmo 1972). Morover, completely different patterns can be found in some reef complexes of Alberta, where gastropods mainly lived in fore-reef environments (Coppold 1976). The taxonomical composition of studied gastropods from the Holy Cross Mountains (see Table 1) is similar to Givetian and Frasnian gastropod faunas from the Harz Mountains and the Rhenish Slate Mountains (Roemer 1843, 1854; Blodgett and Frýda 1999; Frýda 2000; Heidelberger 2001). In the Rheinish Slate Mountains reefs, gastropods are reported mostly from back- and fore-reef facies (Krebs 1974; Burchette 1981; see also Wilson 1975). The taxonomic diversity of the assemblage and associations changed during the Frasnian of the Holy Cross Mountains. At the beginning of Frasnian, there was a remarkable increase in the significance of trochoids and subulitids caused by the general development of the Dyminy reef. In the middle and late Frasnian the contribution of trochoids decreased, on the other hand, the role of euomphaloids, neritoids, and omphalotrochids incresed greatly. The percentage of the representatives of Pleurotomarioidea and Loxonematoidea was greater in the middle Frasnian associations than in the early and late Frasnian ones (Fig. 18).

Gastropod faunas in the Kowala Formation and global events

The evolution of Frasnian gastropod fauna, dwelling on the southern Laurussian shelf, indicates a certain similarity of taxonomic diversity to other benthic groups like brachiopods, rugosans and tabulates (see Racki 1988, 1993a; Nowiński 1993; Wrzołek 1993). The most important element controlling the changes in the carbonate environments were regional depositional cycles caused mainly by eustatic changes of sea level (Racki 1993b; see also McGhee et al. 1991). Mostly, the reef-lagoonal gastropod faunas of the Kowala Formation were very sensitive to bathymetric changes. Practically at the beginning of almost each regional depositional cycle, there was a turnover in the taxonomic composition of the gastropod fauna. The extinction (or emigration) of many species was mainly observed in the middle Givetian and at the beginning of late Givetian in the *Stringocephalus* bank habitats. Biogeographic immigration of new species started from the early Frasnian to the beginning of late Frasnian (Krawczyński 1999; Fig. 2 herein).

Generally, the late Givetian gastropod fauna was poorly diversified. Assemblages of euomphalids, pleurotomarids, and murchisonids, for example *Straparollus* (*Straparollus*) *laevis* from Góra Zamkowa, were developed in the deeper shelf in the late Givetian and at the Givetian–Frasnian bound-

ary interval. There were no changes in the gastropod fauna of the Sitkówka Beds connected with global sea-level rise during the cycle G II (= T–R cycle IIb) and local epeirogenic event G/F III cycle (see Racki 1993b).The following colonization and immigration of the widespread Frasnian species (*Orecopia kadzielniae*, *Westerna subcostata*) appeared together with the evolution of Dyminy reef. Kadzielnia-type mud mounds, with the highly diverse *Euryzone kielcensis* association, were developed below the wave base as a consequence of the transgressive pulse in the *Pa. transitans* Zone (= cycle IIb/c *sensu* Racki 1997). As a result of the next transgressive pulse (= cycle IIc *sensu* Johnson et al. 1985) at the beginning of the *Pa. punctata* Zone, the mud mounds progressively sank and the unique Kadzielnia-type fauna became extinct. In the middle Frasnian, in the north part of the Dyminy reef, the organic buildups were built by large *Stachyodes–Renalcis* colonies, among which fluorished the small gastropods of the *Grabinopsis guerichi* association. The transgressive pulse at the beginning of the late Frasnian (= cycle IId *sensu* Johnson et al. 1985), marked by anoxic lower Kellwasser event in later *Pa. rhenana* Zone, contributed to considerable facies changes and the gradual collapse of the Dyminy reef (see Narkiewicz 1987). Two gastropod associations were developed in the reef-cap phase: *Straparollus* (*Straparollus*) *circularis* and *Naticopsis* (*Naticopsis*) *excentrica*, and also the poorly diversified assemblage *Loxoplocus* (*Donaldiella*) *karczewskii*. The ecosystems of the Dyminy reef finally collapsed at the end of Frasnian as a consequence of the strongest transgressive pulse and the anoxic upper Kellwasser event (Racki and Baliński 1998). The history of gastropods during the Frasnian–Famennian boundary event in the Polish part of the South Laurussia shelf is not exactly known. There is some interruption in the transition to Famennian pelagic sequences in the central part of the Kielce region (stratigraphic gap; see Szulczewski 1995), being probably a last gastropod refugium connected with the central part of the former Dyminy reef. Continuous sequences of the uppermost Frasnian at Kowala and Psie Górki are poor in gastropods. The last Frasnian microdomatid gastropods have been found in silicified brachiopod-crinoid coquinas just below the Frasnian– Famennian boundary at the "Kowala" quarry (see Racki and Baliński 1998). Famennian gastropods from the Holy Cross Mountains occur in cephalopod limestones of Gałęzice and Łagów, for example, cosmopolitan species *Naticopsis* (*Naticopsis*) *inflata* and euomphalids, pleurotomarids as well as loxonemids known from the Famennian (see Sobolev 1911; Dzik 1994). Gastropods are also rare in marly facies at the "Kowala" quarry. Generally, the Famennian gastropods are very poorly investigated, especially the species connected with an impoverished reef environment. Only a few of the Frasnian genera (for example *Naticopsis*) have re-appeared again in the Visean coral-crinoid limestones from Gałęzice (Gromczakiewicz-Łomnicka 1973). The data concerning the Frasnian gastropods of the reef complex, as well as the Famennian gastropods from another parts of the World, have too superficial character (for example, from reef complexes of Canada; see Leavitt 1968; Jamieson 1971; Coppold 1976). Frasnian reef gastropods have not been observed in the Famennian and Early Carboniferous series. Thus, they probably became extinct together with the collapse of the Frasnian reef ecosystem near the Frasnian– Famennian boundary.

Acknowledgements

I am greatly indebted to Prof. Grzegorz Racki (Silesian University) for supervising my Ph.D. thesis, part of which is presented here. Special thanks are due to Prof. Jerzy Dzik (Institute of Paleobiology, Warsaw) and Prof. Stefan W. Alexandrowicz (Academy of Mining and Metalurgy) for reviews of my thesis. I warmly thank Dr. Robert B. Blodgett (Oregon State University) and Dr. Jiři Frýda (Czech Geological Survey, Prague) for review of typescript and language correction. I also thank Prof. Jerzy Dzik for making accessible the gastropod collection of the Institute of Paleobiology, Warsaw, and Dr. Jadwiga Gorczyca-Skała (Wrocław University) for access to the original Gürich collection for my study. I want to thank Dr. Elena Yazykova (Sankt-Petersburg) and Kate and Cris Brownings (Oklahoma) for linguistic assistance. Financial support was given by the Comittee for Scientific Research in Poland (KBN, grant No. 6 P04F 037 11).

References

Bayle, E. 1880. Liste rectificative de quelques noms de genres et d'espèces. *Journal de Conchyliologie* 28: 241–251.

Blodgett, R.B. and Frýda, J. 1999. New Devonian gastropod genera important for paleogeographic reconstructions. *Journal of the Czech Geological Society* 44: 293–308.

Burchette, T.P. 1981. European Devonian reefs: a review of current concepts and models. *Society of Economic Paleontologists and Mineralogists, Special Publication* 30: 85–142.

Chernyshev, F. (Černyšev, F.) 1884. Materials for the research on Devonian Russian sediments [in Russian]. *Trudy Geologičeskogo Komiteta* 1: 1–193.

Chernyshev, F. (Černyšev, F.) 1887. Middle and Upper Devonian fauna of the western Ural [in Russian]. *Trudy Geologičeskogo Komiteta* 3: 28–42.

Chlupáč, I. 1993. Trilobites from the Givetian and Frasnian of the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37 (1992): 395–406.

Coen-Aubert, M. and Wrzołek, T. 1991. Redescription of the rugose coral *Macgeea* (*Rozkowskiella*) *sandaliformis* (Różkowska, 1980) from the Upper Frasnian of the Holy Cross Mountains (Poland). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 61: 5–19.

Cook, A.G. 1995. Sedimentology and depositional environments of the Middle Devonian Big Bend Arkoze and Burdekin Formation, Fanning River Group, Burdekin Subprovince, North Queensland, Australia. *Memoirs of the Queensland Museum* 38: 53–91.

Coppold, M.P. 1976. Buildup to basin transition at the Ancient Wall Complex (Upper Devonian), Alberta. *Bulletin of Canadian Petroleum Geology* 24: 154–192.

Cossmann, M. 1903. Rectifications de nomenclature. *Revue critique de Paléozoologie et Paléophytologie* 7: 67–68.

Donald, J. 1902. On some of the Proterozoic Gastropoda which have been referred to *Murchisonia* and *Pleurotomaria*, with descriptions of new subgenera and species. *Quarterly Journal of the Geological Society of London* 58: 313–339.

Dzik, J. 1994. Evolution of "small shelly fossils" assemblages. *Acta Palaeontologica Polonica* 39: 247–313.

Fischer, P. 1885. Manuel de conchyliologie et de paleontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles. Fasc. 8–9, 689–896. F. Savoy, Paris.

Frýda, J. 2000. Some new Givetian (late Middle Devonian) gastropods from the Paffrath area (Bergisches Land, Germany). *Memoirs of the Queensland Museum* 45: 359–374.

Głuchowski, E. 1993. Crinoid assemblages in the Polish Givetian and Frasnian. *Acta Palaeontologica Polonica* 38: 35–92.

Goldfuss, G.A. 1844. Petrefacta Germaniae et ea, quae in Museo Universitatis Regiae Borussicae Frederichiae Wilhelmiae Rhenanae servantur et alia quaecungue in Museis Hueninghausiano, Muensteriano allisque exstant, iconibus et descriptionobus illustrata. *Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angrenzenden Länder unter Mitwirkung des Herrn Grafen Georg zu Münster.* pt. 3. 252 pp. Arnz & Co., Düsseldorf.

Gordon, M., Jr. and Yochelson, E.L. 1983. A gastropod fauna from the *Cravenoceras hesperium* ammonoid zone (Upper Mississipian) in east-central Nevada. *Journal of Paleontology* 57: 971–991.

Gromczakiewicz-Łomnicka, A. 1973. Visean gastropods from Gałęzice (Holy Cross Mts., Poland) and their stratigraphical value. *Studia Geologica Polonica* 61: 7–54.

Gürich, G. 1896. Das Paläozoikum des Polnischen Mittelgebrige. *Verhandlungen der Russischen Kaiserlichen Gesselschaft zu St.Petersburg II* 32: 1–539.

Hajłasz, B. 1993. Tentaculites from the Givetian and Frasnian of the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37 (1992): 385–394.

Heidecker, E. 1959. Middle Devonian Molluscs from the Burdekin Formation of North Queensland. *University of Queensland Papers, Department of Geology* 5: 3–11.

Heidelberger, D. 2001. Mitteldevonische (Givetische) Gastropoden (Mollusca) aus der Lahnmulde (südliches Rheinisches Schiefergebirge). *Geologische Abhandlungen Hessen* 106: 1–291.

Horný, R. 1952. Two new representants of the family Murchisonidae Koken (Gastropoda) from the Silurian of Central Bohemia [in Czech with English summary]. *Sborník Ústředního Ústavu Geologického; oddíl paleontologický* 19: 209–228.

Hurcewicz, H. 1993. Middle and Late Devonia sponge spicules of the Holy Cross Mountains and Silesian Upland. *Acta Palaeontologica Polonica* 37 (1992): 291–296.

Jamieson, E.R. 1971. Paleoecology of Devonian Reefs in Western Canada. *Proceedings of the North American Paleontological Convention J, September 1969*, 1300–1340.

Johnson, J.G., Klapper, G., and Sandberg, C.A. 1985. Devonian eustatic fluctuations in Euramerica. *Bulletin of the Geological Society of America* 96: 567–587.

Karczewski, L. 1980. Devonian gastropods from the Góry Świętokrzyskie. *Biuletyn Instytutu Geologicznego* 323: 41–55.

Karczewski, L. 1989. Devonian gastopods and bivalves from the Góry Świętokrzyskie Mts. [in Polish with English summary]. *Biuletyn Państwowego Instytutu Geologicznego* 363: 97–133.

Karczewski, L. 1992. Praeheterodonta bivalves from the Devonian of the Góry Świętokrzyskie (Mts.) [in Polish with English summary]. *Prace Państwowego Instytutu Geologicznego* 140: 1–35.

Kaźmierczak, J. 1971. Morphogenesis and systematics of the Devonian Stromatoporoidea from the Holy Cross Mts., Poland. *Palaeontologia Polonica* 26: 1–150.

Keyserling, A. 1846. *Wissenschaftliche Beobachtungen auf einer Reise in das Petschora-Land, im Jahre 1843*, 149–406. Geognostiche Bobachtungen, St. Petersburg.

Kirchner, H.S. 1915. Mitteldevonische Gastropoden von Soetenich in der Eifel. *Verhandlungen des Naturhistorischen Vereins der preussischen Rheinlande und Westfalens* 2: 189–261.

Knight, J.B. 1937. Genotype designations and new names for invalid homonyms among paleozoic gastropod genera. *Journal of Paleontology* 11: 709–714.

Knight, J.B. 1941. Paleozoic gastropod genotypes. *Special Paper Geological Society of America* 32: 1–510.

Knight, J.B. 1945. Some new genera of Paleozoic Gastropoda. *Journal of Paleontology* 19: 573–587.

Knight, J.B. 1956. New families of Gastropoda. *Journal of the Washington Academy of Sciences* 46: 41–42.

Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L., and Robertson, R. 1960. Gastropoda—Systematic Descriptions. *In:* R.C. Moore (ed.), *Treatise on Invertebrate Paleontology, Part I, Mollusca 1*, 169–351. Geological Society of America and University of Kansas, Lawrence, Kansas.

Krawczyński, W. 1998. *Givetian and Frasnian Gastropods from the Polish Part of Southern Laurussia Shelf* [in Polish]. Unpublished Ph.D. thesis. 198 pp. Faculty of Earth Sciences, Silesian University.

Krawczyński, W. 1999. Gastropods from the Givetian and Frasnian of Southern Poland and the global biotic crises [in Polish with English summary]. *Przegląd Geologiczny* 47: 379–383.

Krebs, W. 1974. Devonian carbonate complexes of central Europe. *In:* L.F. Laporte (ed.), Reefs in time and space, selected examples from the recent and ancient. *Special Publication of Society of Economic Paleontologists and Mineralogists* 18: 155–208.

Leavitt, E.M. 1968. Petrology, palaeontology, Carson Creek North Reef Complex, Alberta. *Bulletin of Canadian Petroleum Geology* 16: 298–413.

Linsley, R.M. 1968. Gastropods of the Middle Devonian Anderdon Limestone. *Bulletins of American Paleontology* 54: 333–465.

Malec, J. and Racki, G. 1993. Givetian and Frasnian ostracod asociations from the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37: 359–384.

Mansuy, H. 1912. Étude géologique du Yun-Nan Oriental, II^{e} partie, Paléontologie. *Mémoires du Service Géologique de l'Indo-Chine* 1: 1–146.

M'Coy, F. 1844. *A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland*. 207 pp. Dublin.

McGhee, G.R. Jr. 1996. *The Late Devonian Mass Extinction; the Frasnian–Famennian Crisis*. 303 pp. Columbia University Press, New York.

McGhee, G.R., Jr., Bayer, U., and Seilacher, A. 1991. Biological and evolutionary responses to transgressive-regressive cycles. *In:* G. Einsele, A. Seilacher, and W. Ricken (eds.), *Cycles and Events in Stratigraphy*, 696–708. Springer Verlag, Berlin.

Meek, F.B. 1864. *Palaeontology, I. Section 1. Description of the Carboniferous fossils*. Geological Survey of California, Philadelphia.

Montfort, P.D., de 1810. *Conchyliologie Systématique, et Classification Mathodique des Coquilles; tome 2, Coquilles Univalves, non Cloisonnées*. 676 pp. Paris.

Murray, J.W. 1966. An oil producing reef-fringed carbonate bank in the Upper Devonian Swan Hills Member, Judy Creek, Alberta. *Bulletin of Canadian Petroleum Geology* 14: 1–103.

Narkiewicz, M. 1987. Events on the Late Devonian shelf of Southern Poland and their stratigraphical significance [in Polish]. *Kwartalnik Geologiczny* 31: 581–598.

Nowiński, A. 1993. Tabulate corals from the Givetian and Frasnian of the Holy Cross Mountains and Silesian Upland. *Acta Palaeontologica Polonica* 37 (1992): 183–216.

Pedder, A.E.H. 1966. The Upper Devonian gastropod *Orecopia* in western Canada. *Palaeontology* 9: 142–147.

Phillips, J. 1841. *Figures and desciptions of the Palaeozoic fossils of Cornvall, Devon, and West Somerset; observed in the course of the Ordinance Geological Survey of that district*. 231 pp. Longman, Brown, Green, & Longmans, London.

Playford, P.E. 1980. Devonian "Great Barrier Reef" of Canning Basin, Western Australia. *The American Association of Petroleum Geologists Bulletin* 64: 814–840.

Pusch, G.G. 1837. *Polens Paläontologie oder Abbildung und Beschreibung der vorzüglichsten und der noch unbeschreibenen Petrefakten aus den Gebirgsformationen in Polen, Volhynien und den Karpathen nebst einigen allgemeinen Beiträgen zur Petrefactenkunde und einem Versuch zur Vervollständigung der Geschichte des Europäischen Auer–Ochsen*. 214 pp. Stuttgart.

Racki, G. and Baliński, A. 1998. Late Frasnian Atrypida (Brachiopoda)

from Poland and the Frasnian–Famennian biotic crisis. *Acta Palaeontologica Polonica* 43: 273–304.

Racki, G. and Soboń-Podgórska, J. 1993. Givetian and Frasnian calcareous microbiotas of the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37 (1992): 255–289.

Racki, G. 1988. Middle to Upper Devonian boundary beds of the Holy Cross Mountains, Central Poland: introduction to ecostratigraphy. *Canadian Society of Petroleum Geologists, Memoir* 14 (3): 119–131.

Racki, G. 1990. Frasnian/Famennian event in the Holy Cross Mts, Central Poland: stratigraphic and ecologic aspects. *In:* E.G. Kauffmann and O. Walliser (eds.), Extinction Events in Earth History. *Lecture Notes in Earth Sciences* 30: 169–181. Springer, Berlin.

Racki, G. 1993a. Brachiopod assemblages in the Devonian Kowala Formation of the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37 (1992): 297–357.

Racki, G. 1993b. Evolution of the bank to reef complex in the Devonian of the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37 (1992): 87–182.

Racki, G. 1997. Devonian eustatic fluctuations in Poland. *Courier Forschungsinstitut Senckenberg* 199: 1–12.

Rafinesque, C.S. 1815. *Analyse de la Nature, ou Tableau de l'univers et des corps organisés*. 224 pp. Palermo.

Roemer, F.A. 1843. *Die Versteinerungen des Harzgebirges*. 26–32. Verlag der Hahn'schen Hofbuchhandlung, Hannover.

Roemer, F.A. 1854. Beiträge zur geologischen Kenntniss des norwestlichen Harzgebirges. *Palaeontographica* 3: 1–67.

Różkowska, M. 1980. On Upper Devonian Habitats of Rugose Corals. *Acta Palaeontologica Polonica* 25: 597–611.

Sandberger, G. 1842. Vorläufige Übersicht über die eigenthümlichen bei Villmar ander Lahn auftretenden jüngeren Kalk-Schichten der älteren Formation besonders nach ihren organischen Einschlüssen, und Beschreibung ihren wesentlichsten neuen Arten. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie, und Petrefakten-Kunde* 4: 379–402.

Sandberger, G. and Sandberger, F. 1850–1856. *Die Versteinerungen des Schishtensystems in Nassau*. 564 pp. Kreidel & Niedner, Verlagshandlung, Wiesbaden.

Schlotheim, E.F. 1820. *Die Petrefactenkunde auf ihren jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier-und Pflanzenreichs der Vorwelt erläutert*. 436 pp. Beckerschen Buchhandlung, Gotha.

Siemiradzki, J. 1909. Zejszner's collection from the Devonian of Kielce [in Polish]. *Sprawozdania Komisji Fizjograficznej PAU* 43: 62–94.

Sobolev, D. 1909. Middle Devonian of the Kielce–Sandomierz Region [in Russian]. *Materiâly po geologii Rossii* 24: 41–536.

Sobolev, D. 1911. Famenian of the Kielce–Sandomierz Region [in Russian]. *Ežegodnik po Geologii i Mineralogii Rossii* 13: 34–41.

Sobolev, D. 1912. Upper neo-Devonian from Kielce surroundings [in Russian]. *Izvestâ Varshavskogo Politekhničeskogo Instituta* 1: 1–14.

Stasińska, A. 1953. Genus *Alveolites* Lamarck from Devonian of the Holy Cross Mountains [in Polish]. *Acta Geologica Polonica* 3: 211–237.

Swainson, W. 1840. *A Treatise on Malacology or Shells and Shell-fish*. 420 pp. Longman, London.

Szulczewski, M. and Racki, G. 1981. Early Frasnian bioherms in the Holy Cross Mts. *Acta Geologica Polonica* 31: 147–162.

Szulczewski, M. 1971. Upper Devonian conodonts, stratigraphy and facial development in the Holy Cross Mts. *Acta Geologica Polonica* 21: 1–129.

Szulczewski, M. 1995. Depositional evolution of the Holy Cross Mts. (Poland) in the Devonian and Carboniferousa —review. *Kwartalnik Geologiczny* 39: 449–542.

Ulrich, E.O. and Scofield, W.H. 1897. The lower Silurian Gastropoda of Minnesota. *Geology of Minnesota, Final Report* 3: 813–1081.

Vopni, L.K. and Lerbekmo, J.F. 1972. The Horn Plateau Formation: a Middle Devonian coral reef, Northwest Territories, Canada. *Bulletin of Canadian Petroleum Geology* 20: 498–548.

Walcott, C.D. 1884. Paleontology of the Eureka district (Nevada). *United States Geological Survey Monograph* 8: 1–298.

Walliser, O.H. 1996. Global events in the Devonian and Carboniferous. *In:* O.H. Walliser (ed.), *Global Events and Event Stratigraphy in the Phanerozoic*, 225–250. Springer, Berlin.

Wenz, W. 1938. Gastropoda. Teil 1, Allgemeiner Teil und Prosobranchia (pars.). *In:* O.H. Schindewolf (ed.), *Handbuch der Paläozoologie* 6. 240 pp. Verlag von Gebrüder Borntraeger, Berlin.

Whidborne, G.F. 1889. On some Devonien cephalopods and gasteropods. *The Geological Magazine, New series* 6: 29–30.

Whidborne, G.F. 1891. A monograph of the Devonian fauna of the south of England. The fauna of the limestones of Lummaton, Wolborough, Chircombe Bridge, and Chudleigh. Gastropoda. *The Palaeontographical Society Monographs* 1 (3): 155–250.

Whidborne, G.F. 1892. A monograph of the Devonian fauna of the south of England. The fauna of the limestones of Lummaton, Wolborough, Chircombe Bridge, and Chudleigh. Gastropoda. *The Palaeontographical Society Monographs* 1 (4): 251–344.

Whitfield, R.P. 1886. Notice of a new genus and species of air-breathing mollusk from the Coal measures of Ohio, and observations on *Dawsonella*. *American Journal of Science, 3rd ser.* 21: 123–128.

Wilson, J.L. 1975. *Carbonate Facies in Geologic History*. 471 pp. Springer Verlag, Berlin.

Wrzołek, T. 1988: Tetracoral zonation of the Devonian stromatoporoid-coral limestones in the SW Holy Cross Mountains, Poland. *Canadian Society of Petroleum Geologists, Memoir* 14 (3): 413–424.

Wrzołek, T. 1993. Rugose corals from the Devonian Kowala Formation of the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37 (1992): 217–254.

Ziegler, W. and Sandberg, C.A. 1990. The Late Devonian standard conodont zonation. *Courier Forschungsinstitut Senckenberg* 121: 1–115.